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Integrative Taxonomy Reveals Two New Dragon Millipede Species in the Genus *Desmoxytes* Chamberlin, 1923 from Thailand (Diplopoda: Polydesmida: Paradoxosomatidae)

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ABSTRACT.– Recent field surveys in northern Thailand led to the discovery of two remarkable new species of dragon millipede in the genus *Desmoxytes* Chamberlin, 1923. Using an integrative approach that combined morphological and molecular data, we confirmed the validity of these species, herein described as *Desmoxytes chaofa* Srisonchai, sp. nov. from Mae Hong Son Province and *Desmoxytes sirindhornae* Srisonchai, sp. nov. from Tak Province. To assess their systematic position and relationships, we conducted morphological examinations and reconstructed the phylogeny based on three gene fragments (COI, 16S rRNA, and 28S rRNA). Phylogenetic analysis supports the validity of these two new species, with genetic divergence in the COI gene clearly distinguishing them from congeners, ranging from 10.67–18.67% for *D. chaofa* Srisonchai, sp. nov. and 10.05–17.91% for *D. sirindhornae* Srisonchai, sp. nov. (mean = 14.71%). Notably, the phylogenetic tree aligns well with morphological characters, particularly those of the gonopod. *Desmoxytes chaofa* Srisonchai, sp. nov. is closely related to *D. octoconigera* Srisonchai, Enghoff & Panha, 2018, while *D. sirindhornae* Srisonchai, sp. nov. clusters together with *D. des* Srisonchai, Enghoff & Panha, 2016, both pairs exhibiting similarities in body colouration and gonopod telopodite. Based on current data, these two species are considered as narrow endemics and are restricted to limestone rock wall habitats. Complete morphological illustrations of the two new species and a distribution map of all *Desmoxytes* species are provided.

KEYWORDS: biodiversity, evolution, karst, Southeast Asia, systematics

INTRODUCTION

Recent systematic studies have identified the lineage of dragon millipedes within the family Paradoxosomatidae, comprising eight genera and a total of 84 valid species. These genera include *Alternaxytes* Srisonchai & Enghoff, 2025 (1 species), *Burmaxytes* Srisonchai, Lin & Panha, 2020 (2 species), *Desmoxytes* Chamberlin, 1923 (18 species), *Gigaxytes* Srisonchai, Enghoff & Panha, 2018 (4 species), *Hylomus* Cook & Loomis, 1924 (44 species), *Nagaxytes* Srisonchai, Enghoff & Panha, 2018 (4 species), *Siamaxytes* Srisonchai & Panha, 2024 (1 species), and *Spinaxytes* Srisonchai, Enghoff & Panha, 2018 (10 species) (Srisonchai et al., 2016, 2018a, 2018b, 2018c, 2018d, 2020, 2024, 2025).

Numerous new species of dragon millipedes have been described recently (Liu et al., 2014, 2016; Nguyen et al., 2019; Srisonchai et al., 2018a). The integration of morphological characteristics and molecular data has proven to be a powerful and effective approach for species identification and for evaluating evolutionary relationships, as also demonstrated in other groups of the order Polydesmida (Decker, 2016; Means et al. 2021a, 2021b).

Among the dragon millipedes, *Desmoxytes* is the second most diverse genus, comprising 18 recognized species, as listed in Table 1. This genus can be readily distinguished by the gonopod structure, the pattern of tubercles or spines on the metaterga, and, in some cases, colouration. Srisonchai et al. (2024) confirmed that *Desmoxytes* is a monophyletic group with the morphological characteristics, particularly those of the gonopod and metaterga, aligning well with molecular evidences. Additionally, the phylogenetic results show a clear correspondence with the species' geographical distribution, with closely related lineages generally confined to the same or adjacent regions.

Almost all *Desmoxytes* species inhabit limestone areas and are highly localized to natural forests. Despite significant progress in millipede research in Thailand, further surveys in unexplored areas of the country, especially karst, remain essential. Unveiling the full diversity of *Desmoxytes* across mainland Southeast Asia requires extensive collecting efforts, particularly in underexplored and remote regions of the country, which should be prioritized to uncover additional hidden biodiversity (Clements et al., 2006).

In 2024, two distinct *Desmoxytes* morphotypes were discovered exclusively on the rock walls of limestone karsts in northern Thailand during the fieldworks. Based on their general appearance, these morphotypes are clearly different from other known dragon millipedes. In the present study, we describe them as

TABLE 1. Species of *Desmoxytes* and their current distribution.

Species of *Desmoxytes*	Type locality	Distribution (Province)	Reference
1. *D. aurata* Srisonchai, Enghoff & Panha, 2018	Thailand, Surat Thani Province, Kanchanadit District, Khao Phanom Wang Cave	Surat Thani	Srisonchai et al. (2018)
2. *D. breviverpa* Srisonchai, Enghoff & Panha, 2016	Thailand, Phrae Province, Long District, Sareethai Cave	Phrae, Lampang, Uttaradit	Srisonchai et al. (2016) and Srisonchai et al. (2018)
3. *D. cervina* (Pocock, 1895)	Myanmar, South Tenasserim	Myanmar (near Myeik), Thailand (Chumphon, Krabi, Nakhon Si Thammarat, Phang Nga, Phuket, Ranong, Surat Thani)	Pocock (1895), Srisonchai et al. (2018)
4. *D. corythosaurus* Srisonchai, Enghoff & Panha, 2018	Thailand, Surat Thani Province, Phanom District, Ban Song Phi Nong	Surat Thani	Srisonchai et al. (2018)
5. *D. delfae* (Jeekel, 1964)	Thailand, Bukit Besar (Satun Province)	Krabi, Nakhon Si Thammarat, Phatthalung, Satun, Songkhla, Surat Thani, Trang, Yala	Jeekel (1964), Srisonchai et al. (2018)
6. *D. des* Srisonchai, Enghoff & Panha, 2016	Thailand, Chiang Mai Province, Fang District, Doi Angkhang, near Royal Agricultural Station	Chiang Mai	Srisonchai et al. (2016) and Srisonchai et al. (2018)
7. *D. euros* Srisonchai, Enghoff & Panha, 2018	Thailand, Chanthaburi Province, Kaeng Hang Maeo District, Khao Wong Kot Cave	Chanthaburi, Chonburi, Rayong, Sa Kaeo	Srisonchai et al. (2018)
8. *D. flabella* Srisonchai, Enghoff & Panha, 2018	Thailand, Trang Province, Palian District, Tham Khao Ting	Trang	Srisonchai et al. (2018)
9. *D. golovatchi* Srisonchai, Enghoff & Panha, 2018	Thailand, Kanchanaburi Province, Thong Pha Phum District, Prang Ka Sri Temple	Kanchanaburi	Srisonchai et al. (2018)
10. *D. octoconigera* Srisonchai, Enghoff & Panha, 2018	Thailand, Kanchanaburi Province, Sangkhla Buri District, Wat Tham Kaeo Sawan Bandal	Kanchanaburi	Srisonchai et al. (2018)
11. *D. perakensis* Srisonchai, Enghoff & Panha, 2018	Malaysia, Perak, Ipoh, Ulu Kinta, near The Lost World Tambun Theme Park	Malaysia (Perak)	Srisonchai et al. (2018)
12. *D. pinnasquali* Srisonchai, Enghoff & Panha, 2016	Thailand, Phitsanulok Province, Noen Maprang District, near Pra Tham Mans Monastery (Tham Wangdaeng)	Phitsanulok	Srisonchai et al. (2016) and Srisonchai et al. (2018)
13. *D. planata* (Pocock, 1895)	Myanmar, Andaman Sea, Great Cocos Island	Wide distribution	Pocock (1895), Srisonchai et al. (2018)
14. *D. purpurosea* Enghoff, Sutcharit & Panha, 2007	Thailand, Uthai Thani Province, Department of National Parks, Tam Pratun Non-Hunting Area, Hup Pa Tard	Kanchanaburi, Lamphun Suphan Buri, Uthai Thani	Enghoff et al. (2007), Srisonchai et al. (2018)
15. *D. takensis* Srisonchai, Enghoff & Panha, 2016	Thailand, Tak Province, Phobphra District, Nangkruen Waterfall	Kamphaeng Phet, Tak	Srisonchai et al. (2016) and Srisonchai et al. (2018)
16. *D. taurina* (Pocock, 1895)	Myanmar, Pegu (Taikkyii and Palon)	Myanmar (Pegu)	Pocock (1895)
17. *D. terae* (Jeekel, 1964)	Malaysia, Perlis, Kaki Bukit, near Kampong Wang Tangga	Malaysia (Perlis), Thailand (Satun)	Jeekel (1964)
18. *D. waepyanensis* Srisonchai, Enghoff & Panha, 2018	Myanmar, Kayin State, 12 km south of Kamarmuang City, Wae Pyan Cave	Myanmar (Kayin State)	Srisonchai et al. (2018)

two new *Desmoxytes* species, incorporating both morphological and phylogenetic data.

MATERIALS AND METHODS

Specimen collection and preservation

Specimens were collected from natural limestone habitats in northern Thailand in August, with detailed locality information available in Table 2. All specimens were euthanized using a 5% ethyl alcohol solution in compliance with ethical standards, following the guidelines of the American Veterinary Medical Association (American Veterinary Medical Association, 2020). Post-euthanasia, specimens were preserved in either 70% ethanol for morphological examinations or 95% ethanol for DNA analysis.

Fieldwork conducted in restricted areas was authorized by the Department of National Parks, Wildlife, and Plant Conservation of Thailand (Permit Nos. 23103 and 23104). Additionally, this study was approved by the Institutional Animal Care and Use Committee of Khon Kaen University (Approval No. IACUC-KKU-32/65).

Illustrations

During fieldwork, live specimens were photographed using a Canon 90D digital camera equipped with a Canon EF 100mm f/2.8 Macro USM lens. Specimens for scanning electron microscopy (SEM) were dissected under a stereo microscope, mounted on aluminium stubs, coated with gold, and then imaged. After SEM analysis, the specimens were preserved in 70% ethanol. All image plates were created and arranged using Adobe Photoshop 2021, while the background for the distribution map was sourced from the Elastic Terrain Map (Willett et al., 2015).

Morphological study

Morphological comparisons, terminology, and descripttions were primarily derived from existing literature (Srisonchai et al., 2016, 2018a). A thorough comparison of morphological characteristics was conducted by examining holotypes and paratypes of available dragon millipede species to assess the relationship between the two new species and their congeners.

Morphological abbreviations. blm = broad lobe of lamina medialis, cx = coxa, ca = cannula, dlm = distal lobe of lamina medialis, fe = femoral part, ll = lamina lateralis, lm = lamina medialis, ms = mesal sulcus, pfe = prefemur, plm = process on lamina medialis, pof = postfemoral part, sg = seminal groove, sl = solenomere, sph = solenophore.

Institutional abbreviations

ASRU = Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand; CUMZ = Chulalongkorn University Museum of Zoology, Bangkok, Thailand; MZKKU = Zoological Museum of Khon Kaen University, Khon Kaen, Thailand; NHMD = Natural History Museum of Denmark, Copenhagen, Denmark; NHMUK = Natural History Museum, London, United Kingdom; NHMW = Naturhistorisches Museum Wien, Vienna, Austria; ZFMK = Zoological Research Museum Koenig, Bonn, Germany.

DNA extraction and alignments

Genomic DNA was extracted from the legs and a few body rings using the NucleoSpin Tissue Kit (Machery-Nagel), following the manufacturer's instructtions. To sequence three gene fragments from both mitochondrial and nuclear DNA—Cytochrome C Oxidase Subunit I (COI), 16S ribosomal RNA (16S rRNA), and 28S ribosomal RNA (28S rRNA)—a Polymerase Chain Reaction (PCR) amplification was performed, covering a total of 1,533 base pairs (bp). PCR amplification was carried out using three primer sets: LCO1490 and HCO2198 for COI (Folmer et al., 1994), 16Sar and 16Sbr for 16S rRNA (Simon et al., 1994), and 28Sa and 28Sb for 28S rRNA (Colgan et al., 2000). The PCR reaction mixture had a total volume of 40 µL, comprising 16 µL of EmeraldAmp GT PCR Master Mix, 12 µL of ddH2O, 8 µL of primers (4 µL each), and 4 µL of DNA template. The amplification process included an annealing phase at 47–49°C for 1 minute, followed by a 2-minute extension at 72°C. To verify successful amplification of COI fragments, PCR products were checked in 1% agarose gel electrophoresis with 1X TBE buffer and visualized under UV trans-illumination. All PCR products were subsequently purified, and the sequencing of target genes was conducted using Sanger sequencing at Bioneers Co. (Korea).

Chromatogram sequences were edited and examined in MEGA 7 (Kumar et al., 2016), with particular attention given to detecting stop codons for COI and correcting misaligned regions. The finalized nucleotide sequences for all taxa are listed in Table 2 and all have been deposited in GenBank under accession numbers PV770138–PV770150 for COI, PV788851–PV788865 for 16S and PV788837–PV788850 for 28S. Sequence alignments were performed separately using ClustalW in MEGA 7. The data set was analysed using a five-partition scheme, distinguishing three codon positions of COI, as well as each individual partition for 16S rRNA and 28S rRNA.

TABLE 2. Lists of specimens analysed in this study in relation to their voucher code, locality, GenBank accession number and reference.

Species	Voucher code	Locality	COI	16S	28S	Reference
Outgroup						
1. *Gigaxytes gigas* (Golovatch & Enghoff, 1994)	CUMZ (DNA px-K1)	Wat Khao Hua Sing, Plai Phraya District, Krabi Province, Thailand	OR765908	OR771526	OR771613	Srisonchai et al. (2024)
2. *Hylomus rhinoceros* (Likhitrakarn et al., 2015)	CUMZ (DNA px-E12)	Ban Thongvay, Paksong, Bolaven Plateau, Champasak Province, Laos	OR765913	OR771529	OR771619	Srisonchai et al. (2024)
3. *Nagaxytes erecta* Srisonchai et al., 2018	CUMZ (DNA px-C7)	Wat Pak Lam Pilock, Thong Pha Phum District, Kanchanaburi Province, Thailand	OR765918	OR771534	OR771624	Srisonchai et al. (2024)
4. *Orthomorpha* cf. *pterygota* Golovatch, 1998	CUMZ (DNA px-K9)	Tham Boon Raksa Phu Pha Ram, Lam Thap District, Krabi Province, Thailand	OR765930	OR771549	OR771639	Srisonchai et al. (2024)
5. *Pogonosternum adrianae* (Jeekel, 1982)	NMV K-12203	23 km S of Dargo, Mitchell River National Park, Victoria, Australia	KU745235	KU745194	KU745185	Srisonchai et al. (2024)
6. *Pogonosternum laetificum* (Jeekel, 1982)	SMNG VNR016987	Marysville State Forest, 5.8 km SE of Narbethong, Acheron Way, Victoria, Australia Australia	KU745244	KU745203	KU745187	Srisonchai et al. (2024)
7. *Siamaxytes bifurca* Srisonchai et al., 2024	CUMZ (DNA px-C14)	Wat Tham Sue Dao, Sai Yok District, Kanchanaburi Province, Thailand	OR765935	OR771552	OR771644	Srisonchai et al. (2024)
Ingroup – genus *Desmoxytes*						
8. *D. aurata*	CUMZ (DNA px-95)	Khao Phanom Wang Cave, Kanchanadit District, Surat Thani Province, Thailand	OR765866	OR771486	OR771570	Srisonchai et al. (2024)
9. *D. aurata*	CUMZ (DNA px-96)	Khao Phanom Wang Cave, Kanchanadit District, Surat Thani Province, Thailand	OR765867	OR771487	OR771571	Srisonchai et al. (2024)
10. *D. breviverpa*	CUMZ (DNA px-48)	Sareethai Cave, Long District, Phrae Province, Thailand	OR765868	OR771488	OR771572	Srisonchai et al. (2024)
11. *D.breviverpa*	CUMZ (DNA px-53)	Sareethai Cave, Long District, Phrae Province, Thailand	OR765869	OR771489	OR771573	Srisonchai et al. (2024)
12. *D. cervina*	CUMZ (DNA px-B4)	Wat Suwan Khuha (Monkey Cave), Takua Thung District, Phang Nga Province, Thailand	OR765870	OR771490	OR771574	Srisonchai et al. (2024)
13. *D. cervina*	CUMZ (DNA px-B6)	Ban Song Phi Nong, Phanom District, Surat Thani Province, Thailand	OR765871	OR771491	OR771575	Srisonchai et al. (2024)
14. *D. cervina*	CUMZ (DNA px-B7)	Phung Chang Cave, Mueang Phang Nga District, Phang Nga Province, Thailand	OR765872	OR771492	OR771576	Srisonchai et al. (2024)
15. *D. cervina*	CUMZ (DNA px-K2)	Wat Khao Hua Sing, Plai Phraya District, Krabi Province, Thailand	OR765873	OR771493	OR771577	Srisonchai et al. (2024)
16. *D. chaofa* sp. nov.	MZKKU (KS164)	Pha Daeng Cave, Mueang District, Mae Hong Son, Thailand	PV786138	PV788851	PV788837	This study
17. *D. chaofa* sp. nov.	MZKKU (KS165)	Pha Daeng Cave, Mueang District, Mae Hong Son, Thailand	PV786139	PV788852	PV788838	This study
18. *D. chaofa* sp. nov.	MZKKU (KS167)	Pha Daeng Cave, Mueang District, Mae Hong Son, Thailand	PV786140	PV788853	PV788839	This study
19. *D. chaofa* sp. nov.	MZKKU (KS168)	Pha Daeng Cave, Mueang District, Mae Hong Son, Thailand	PV786141	PV788854	PV788840	This study
20. *D. chaofa* sp. nov.	MZKKU (KS169)	Pha Daeng Cave, Mueang District, Mae Hong Son, Thailand	PV786142	PV788855	PV788841	This study
21. *D. corythosaurus*	CUMZ (DNA px-17)	Wat Tham Wararam, Phanom District, Surat Thani Province, Thailand	OR765874	OR771494	OR771578	Srisonchai et al. (2024)
22. *D. delfae*	CUMZ (DNA px-M2)	Wat Khao Rup Chang, Sa Dao District, Songkla Province, Thailand	OR765875	OR771495	OR771579	Srisonchai et al. (2024)
23. *D. delfae*	CUMZ (DNA px-M3)	Wat Khao Rup Chang, Sa Dao District, Songkla Province, Thailand	OR765876	OR771496	OR771580	Srisonchai et al. (2024)
24. *D. des*	CUMZ (DNA px-DAK)	Doi Angkhang, near Royal Agricultural Station, Fang District, Chiang Mai Province, Thailand	OR765877	OR771497	PV788842	Srisonchai et al. (2024), this study
25. *D. des*	MZKKU (KS154)	Wat Tham Krab, Chiang Dao District, Chiang Mai Province, Thailand	PV786143	PV788856	PV788843	This study
26. *D. des*	MZKKU (KS156)	Wat Tham Krab, Chiang Dao District, Chiang Mai Province, Thailand	PV786144	PV788857	PV788844	This study
27. *D. euros*	CUMZ (DNA px-160)	Khao Wong Kot Cave, Kaeng Hang Maeo District, Chanthaburi Province, Thailand	OR765878	OR771498	OR771581	Srisonchai et al. (2024)
28. *D. euros*	CUMZ (DNA px-161)	Khao Wong Kot Cave, Kaeng Hang Maeo District, Chanthaburi Province, Thailand	OR765879	OR771499	OR771582	Srisonchai et al. (2024)
29. *D. flabella*	CUMZ (DNA px-212)	Tham Khao Ting, Palian District, Trang Province, Thailand	OR765880	OR771500	OR771583	Srisonchai et al. (2024)
30. *D. flabella*	CUMZ (DNA px-213)	Tham Khao Ting, Palian District, Trang Province, Thailand	OR765881	OR771501	OR771584	Srisonchai et al. (2024)

TABLE 2. Continued.

Species	Voucher code	Locality	COI	16S	28S	Reference
30. *D. flabella*	CUMZ (DNA px-213)	Tham Khao Ting, Palian District, Trang Province, Thailand	OR765881	OR771501	OR771584	Srisonchai et al. (2024)
31. *D. golovatchi*	CUMZ (DNA px-A4)	Prang Ka Sri Temple, Thong Pha Phum District, Kanchanaburi Province, Thailand	OR765882	OR771502	OR771585	Srisonchai et al. (2024)
32. *D. golovatchi*	CUMZ (DNA px-B15)	Prang Ka Sri Temple, Thong Pha Phum District, Kanchanaburi Province, Thailand	OR765883	OR771503	OR771586	Srisonchai et al. (2024)
33. *D. octoconigera*	CUMZ (DNA px-A10)	Wat Tham Kaeo Sawan Bandal, Sangkhla Buri District, Kanchanaburi Province, Thailand	OR793305	OR771504	OR771587	Srisonchai et al. (2024)
34. *D. octoconigera*	CUMZ (DNA px-A11)	Wat Tham Kaeo Sawan Bandal, Sangkhla Buri District, Kanchanaburi Province, Thailand	OR793306	OR771505	OR771588	Srisonchai et al. (2024)
35. *D. pinnasquali*	CUMZ (DNA px-55)	Tham Wangdaeng, Noen Maprang District, Phitsanulok Province, Thailand	OR765884	PV788858	OR771589	Srisonchai et al. (2024), this study
36. *D. pinnasquali*	CUMZ (DNA px-59)	Tham Wangdaeng, Noen Maprang District, Phitsanulok Province, Thailand	OR765885	PV788859	OR771590	Srisonchai et al. (2024), this study
37. *D. pinnasquali*	MZKKU (KS188)	Phra Sai Ngam Cave, Noen Maprang District, Phitsanulok Province, Thailand	PV786145	PV788860	PV788845	This study
38. *D. pinnasquali*	MZKKU (KS189)	Phra Sai Ngam Cave, Noen Maprang District, Phitsanulok Province, Thailand	PV786146	PV788861	PV788846	This study
39. *D. planata*	CUMZ (DNA px-2)	Thong Pha Phum Forest Garden, Thong Pha Phum District, Kanchanaburi Province, Thailand	OR765886	OR771506	OR771591	Srisonchai et al. (2024)
40. *D. planata*	CUMZ (DNA px-159)	Ngawub Chuang River, Myeik, Myanmar	OR765887	OR771507	OR771592	Srisonchai et al. (2024)
41. *D. planata*	CUMZ (DNA px-A22)	Wat Paung Malai (Wat Tham Khao Iko), Khao Yoi District, Phetchaburi Province, Thailand	OR765888	OR771508	OR771593	Srisonchai et al. (2024)
42. *D. purpurosea*	CUMZ (DNA px-119)	Hup Pa Tard, Lansak District, Uthai Thani Province, Thailand	OR765889	OR771509	OR771594	Srisonchai et al. (2024)
43. *D. purpurosea*	CUMZ (DNA px-120)	Hup Pa Tard, Lansak District, Uthai Thani Province, Thailand	OR765890	OR771510	OR771595	Srisonchai et al. (2024)
44. *D. purpurosea*	CUMZ (DNA px-126)	Tham Than Lod Cave, Chalermrattanakosin National Park, Si Sawat District, Kanchanaburi Province, Thailand	OR765891	OR771511	OR771596	Srisonchai et al. (2024)
45. *D. sirindhornae* sp. nov.	MZKKU (KS159)	Nam Ook Roo Monastery, Tha Song Yang District, Tak Province, Thailand	PV786147	PV788862	PV788847	This study
46. *D. sirindhornae* sp. nov.	MZKKU (KS160)	Nam Ook Roo Monastery, Tha Song Yang District, Tak Province, Thailand	PV786148	PV788863	PV788848	This study
47. *D. sirindhornae* sp. nov.	MZKKU (KS161)	Nam Ook Roo Monastery, Tha Song Yang District, Tak Province, Thailand	PV786149	PV788864	PV788849	This study
48. *D. sirindhornae* sp. nov.	MZKKU (KS162)	Nam Ook Roo Monastery, Tha Song Yang District, Tak Province, Thailand	PV786150	PV788865	PV788850	This study
49. *D. takensis*	CUMZ (DNA px-063)	Nangkrun Waterfall, Phobphra District, Tak Province, Thailand	OR765892	OR771512	OR771597	Srisonchai et al. (2024)
50. *D. takensis*	CUMZ (DNA px-064)	Nangkrun Waterfall, Phobphra District, Tak Province, Thailand	OR765893	OR771513	OR771598	Srisonchai et al. (2024)
51. *D. takensis*	CUMZ (DNA px-136)	Chao Por Phawo Shrine, Mae Sot District, Tak Province, Thailand	OR765894	OR771514	OR771599	Srisonchai et al. (2024)
52. *D. terae*	CUMZ (DNA px-220)	Tham Tone Din (Tone Din Cave), Thale Ban National Park, Khuan Don District, Satun Province, Thailand	OR765895	OR771515	OR771600	Srisonchai et al. (2024)
53. *D. terae*	CUMZ (DNA px-M9)	Tham Tone Din (Tone Din Cave), Thale Ban National Park, Khuan Don District, Satun Province, Thailand	OR765896	OR771516	OR771601	Srisonchai et al. (2024)
54. *D. waepyanensis*	CUMZ (DNA px-143)	Wae Pyan Cave, 12 km south of Kamarmuang City, Kayin State, Myanmar	OR765897	OR771517	OR771602	Srisonchai et al. (2024)
55. *D. waepyanensis*	CUMZ (DNA px-144)	Wae Pyan Cave, 12 km south of Kamarmuang City, Kayin State, Myanmar	OR765898	OR771518	OR771603	Srisonchai et al. (2024)

To identify the most suitable models for Bayesian inference (BI) and maximum likelihood (ML) analyses, ModelFinder ver 1.4.2 and PartitionFinder ver 2.1.1 were employed (Lanfear et al., 2012; Kalyaanamoorthy et al., 2017). The three gene datasets were then concatenated in Kakusan4 (Tanabe 2011).

Genetic distances for the COI gene were calculated using the *p*-distance method in MEGA 7 (Kumar et al. 2016) under Kimura-2 parameter model and pairwise deletion parameter.

Phylogenetic reconstruction

A total of 42 new sequences were generated in this study. We analysed 55 taxa, including 18 ingroup species and 7 outgroup species, as detailed in Table 2. The outgroups were from subfamily Australiosomatinae (*Pogonosternum adrianae* (Jeekel, 1982); *Pogonosternum laetificum* (Jeekel, 1982)) and subfamily Paradoxosomatinae (*Gigaxytes gigas* (Golovatch & Enghoff, 1994); *Hylomus rhinoceros* (Likhitrakarn et al., 2005); *Nagaxytes erecta* Srisonchai et al., 2018; *Orthomorpha* cf. *pterygota* Golovatch, 1998; *Siamaxytes bifurca* Srisonchai et al., 2024).

Two phylogenetic approaches including Bayesian inference (BI) and maximum likelihood (ML) were computed via the CIPRES Science Gateway. BI analysis was conducted in MrBayes on XSEDE 3.2.7a (Ronquist et al., 2012) with Markov Chain Monte Carlo (MCMC) algorithms, employing a randomly generated starting tree. The analysis ran for 20 million generations, with sampling occurring every 1,000 generations. ML analysis was performed using IQ-TREE on XSEDE 1.6.6 (Minh et al., 2020) with 10,000 ultrafast bootstrap replicates (UFBoot).

The resulting ML and BI trees were visualized and refined in FigTree v.1.4.0 (Rambaut 2010), followed by graphical processing in Adobe Illustrator 2021. Nodal support was considered strong when BI posterior probabilities (PP) were greater than 0.95 and ML bootstrap values (BS) exceeded 70% (Huelsenbeck & Hillis 1993; Larget & Simon 1999).

RESULTS

Sequence annotations and distances

The final aligned gene sequences consisted of the following: the COI gene was 658 base pairs (bp) long, including 322 variable sites, 336 conserved sites, with 284 of the variable sites being parsimony-informative. The 16S rRNA gene alignment (584 bp including gaps) contained 331 variable sites and 204 conserved sites, with 304 parsimony-informative sites. The 28S rRNA gene alignment (356 bp including gaps) included 35 variable sites and 305 conserved sites, with 22 parsimony-informative sites. As a result, the concatenated data set comprised a total of 1,533 aligned characters.

The interspecific genetic distances (uncorrected *p*-distances) for the partial COI gene within the genus *Desmoxytes* ranged from 3.23% to 20.36% (see Table A1). Specifically, the percentual genetic divergence between the two newly described species and congeners were 10.67% to 18.67% in *D. chaofa* sp. nov. and 10.05% to 17.91% in *D. sirindhornae* sp. nov.

Phylogenetic tree

The phylogenetic tree constructed using Bayesian inference (BI) and maximum likelihood (ML) analyses exhibited a largely consistent topology (Fig. 1 and Fig. A1), with minor differences observed in some intermediate nodes. The BI tree was chosen as the primary visualization due to its strong support across nearly all branches. Both analyses confirmed that all *Desmoxytes* species form a well-supported monophyletic group (PP = 0.96, BS = 83), and that individuals within each species clustered into their own distinct, well-supported clades (PP = 1, BS = 100).

Two newly described species, *D. chaofa* sp. nov. and *D. sirindhornae* sp. nov., were phylogenetically identified. *Desmoxytes chaofa* sp. nov. forms a clade with *D. octoconigera* Srisonchai et al., 2018, showing a COI genetic divergence of 13.45–13.50% with strong support (PP = 0.98, BS = 92). Together, these two species are sister taxa to a distinctive clade of *Desmoxytes* species (*D. breviverpa* Srisonchai et al., 2016; *D. golovatchi* Srisonchai et al., 2018; *D. purpurosea* Enghoff et al., 2007; *D. takensis* Srisonchai et al., 2016; *D. waepyanensis* Srisonchai et al., 2018), exhibiting a striking purple/pink/red body colouration and supported by strong statistical values (PP = 0.98, BS = 90). In contrast, *D. sirindhornae* sp. nov. clustered closely with *D. des* Srisonchai et al., 2016 with COI genetic divergence ranging from 10.77–17.77%, forming a distinct clade from all other *Desmoxytes* species. This distinct grouping is supported not only by strong phylogenetic support (PP = 1, BS = 97), but also by shared morphological characters, including metaterga 2–19 with 2+2 setiferous tubercles in both anterior and posterior rows and brownish pink to pink paraterga contrasting with the brown body colour.

Description of new species

Class Diplopoda de Blainville in Gervais, 1844
Order Polydesmida Leach, 1815
Family Paradoxosomatidae Daday, 1889
Genus *Desmoxytes* Chamberlin, 1923

***Desmoxytes chaofa* Srisonchai, sp. nov.**
https://zoobank.org/urn:lsid:zoobank.org:act: 3EF23B9A-2640-4028-BB16-EB7E96A4DE32
(Figs 2–6)

Desmoxytes planata — Srisonchai et al., 2018: 118.

Material examined.– Holotype: Male (MZKKU) THAILAND, Mae Hong Son Province, Mueang District, Pha Daeng Cave, 19°25'22.9"N 97°59'03.1"E, ca. 300 m a.s.l., coll. R. Srisonchai, K. Srikampha and

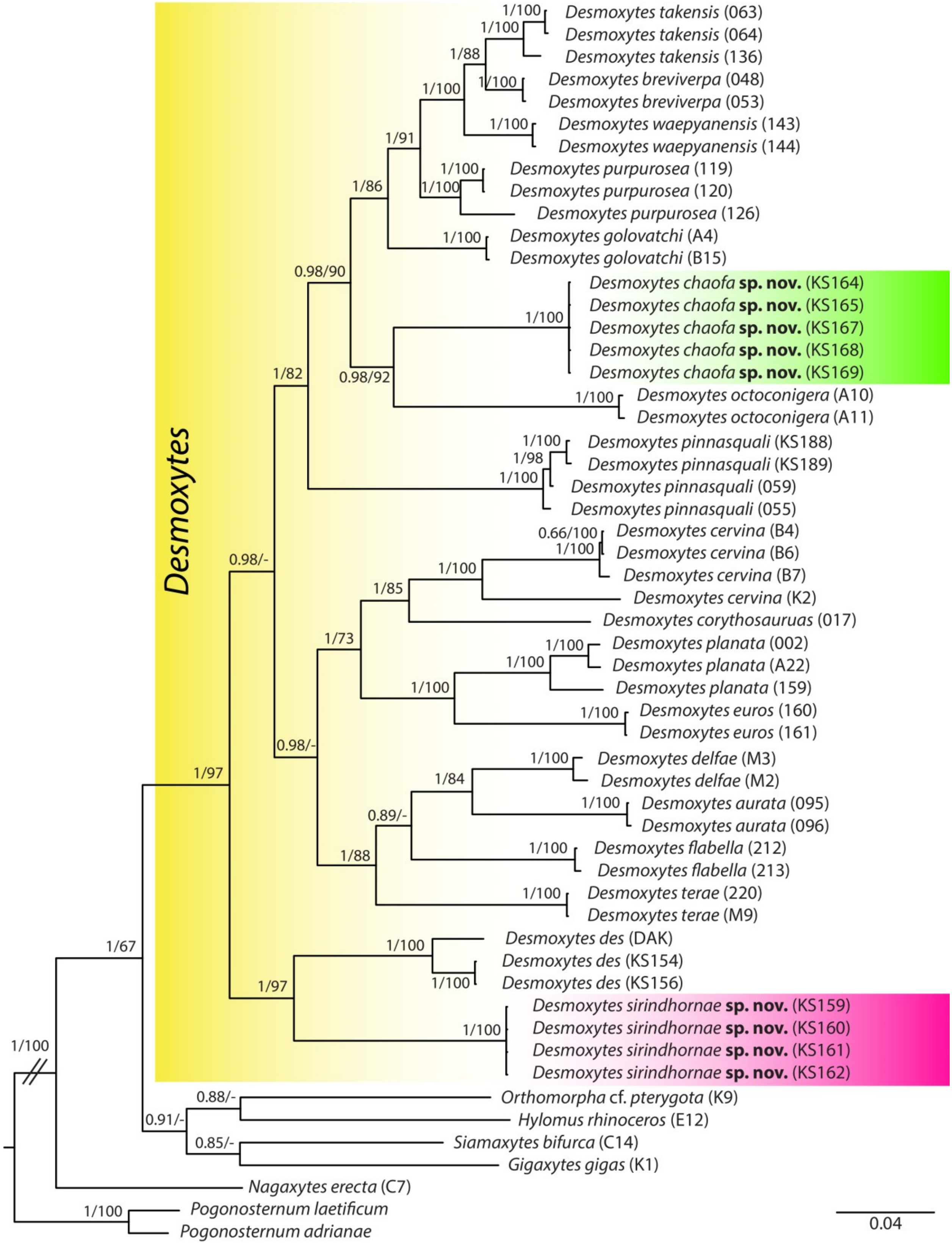

FIGURE 1. Phylogenetic tree based on Bayesian inferences (BI) of the concatenated data set (COI + 16S rRNA + 28S rRNA). Numbers on nodes indicate Bayesian posterior probabilities (PP) from BI/ bootstrap support (BS) from ML. The dash "-" at the nodes refers to a different topology in the BI analysis compared to ML (see Supplemental File 2). Numbers in parentheses following species names represent the voucher codes of the specimens. Colours denote the two new species (*Desmoxytes chaofa* sp. nov. and *Desmoxytes sirindhornae* sp. nov.). Scale bar represents p-distance, indicating the scale of genetic change (measured as nucleotide substitutions per site).

T. Benchapong, 10 August 2024. Paratypes: 20 males, 31 females (MZKKU), same data as holotype. 1 male, 1 female (CUMZ), same data as holotype. 1 male, 1 female (NHMD), same data as holotype. 1 male, 1 female (NHMUK), same data as holotype. 1 male, 1 female (NHMW), same data as holotype. 1 male, 1 female (ZFMK), same data as holotype.

Other material examined (not type) from Srisonchai et al. (2018).– 12 males, 12 females (CUMZ), Mueang Mae Hong Son District, Tham Pla-Namtok Pha Suea National Park, 19°30'07"N, 98°00'23"E, ca. 398 m a.s.l., 19 July 2008, leg. ASRU members. 9 males, 14 females (CUMZ), THAILAND, Mae Hong Son Province, Mueang Mae Hong Son District, Tham Phadaeng, 19°25'23"N, 97°59'04"E, ca. 288 m a.s.l., 19 September 2008, leg. ASRU members.

Etymology.– The originally Thai term 'chaofa', a noun in apposition, signifies a royal princess of the Thai monarchy and is bestowed in honour of Her Royal Highness Princess Maha Chakri Sirindhorn. Renowned for her dedication to biodiversity research and environmental conservation, she has made significant contributions to these fields. With a profound passion for science and nature, she has actively supported research initiatives that deepen the understanding and preservation of Thailand's rich biodiversity.

Diagnosis.– Metaterga 2–19 with conspicuous cones/ spines in posterior row. Similar in this respect to *D. breviverpa*, *D. golovatchi*, *D. octoconigera*, *D. pinnasquali*, *D. purpurosea*, *D. takensis* and *D. taurina*, but the new species differs from these species (except *D. octoconigera*) by the combination of the following characters: dark brown body colour (*vs* bright purple/ pink/red/pinkish brown) and distal part of gonopod telopodite (postfemoral part + solenophore) being more slender (*vs* more stout). The new species can be distinguished from *D. octoconigera* by metaterga 2–19 with 2+2 cones in anterior row and 2+2 cones/spines in posterior row (*vs* 4+4 cones in both anterior and posterior rows).

Description.–

Size (Fig. 2A–C). Length 18–22 mm (male), 20–28 mm (female); width of midbody metazona ca. 1 mm (male), ca. 1.2 mm (female). Width of head < ring 2 = 3 < 4 < collum < 5–17, thereafter body gradually tapering towards telson.

Colour (Fig. 2A–C). Specimens in life dark brown; head, prozona, metaterga and surface below paraterga dark brown; antenna, paraterga, telson, sterna and legs brown; a few basal podomeres whitish brown.

Head (Figs 2A–C; 3A, D, H, I). Vertex bare. Epicranial suture conspicuous on vertex. Labrum and clypeus sparsely setose. Mouthparts not dissected, typical as in paradoxosomatids.

Antennae (Figs 2A–C; 3J, K). Very long and slender, reaching backward to rings 5–6 in male and 4–5 in female when stretched dorsally; antennomeres 5–7 with short sensilla near distal part; antennomere 8 with four conical sensilla.

Collum (Figs 3A, L; 4A). With 4+4 setiferous tubercles in anterior row, 1+1 setiferous tubercles in intermediate row and 2+2 setiferous tubercles in posterior row. All tubercles in posterior row larger than anterior and intermediate ones. Paraterga of collum elevated at about 20° and directed caudolaterad; lateral margin with one setiferous notch on each side; tip acute.

Tegument (Figs 4F–I; 5A). Prozona finely shagreened. Metaterga, base of paraterga and surface below paraterga with microgranulation. Paraterga, sterna and telson smooth.

Spiracles (Fig. 4B, C). Ovoid; with small spiracular filters consisting of fingerlike structures.

Metaterga (Figs 3A–C; 4F, G). Metaterga 2–19 with 2+2 setiferous tubercles/cones in anterior row and 2+2 setiferous cones/spines in posterior row. Outer spines of posterior row longer than inner one. Suture between prozona and metazona shallow and wide. Axial line inconspicuous. Sulcus on metaterga shallow and wide, conspicuous on rings 5–18.

Limbus of midbody ring (Fig. 4J, K). Conspicuous; with rows of very long filaments, fused together and forming an anteroposteriorly striate lamella; margin finely spiculate, spicules equal in size.

Paraterga (Figs 3A–C, E–G, M; 4D, E). Paraterga of rings 2–17 strongly developed, winglike; paraterga of rings 18–19 gradually tapering towards telson. Elevated at about 50° (male) and 40° (female); directed caudolaterad; lateral margin with two conspicuous setiferous notches; on pore-bearing rings sometimes with a tiny notch located just next to ozopore, close to the tip; tip acute. Ozopore conspicuous, oval, located at about half of midbody length of paraterga.

Pleurosternal keels (Fig. 4A). Conspicuous, simple, long ridges on rings 2; small conspicuous ridge on ring 3; thereafter missing.

Telson (Fig. 4L–O). Preanal ring with conspicuous conical epiproct; lateral setiferous tubercles short; apical tubercles conspicuous; tip slightly concave; spinnerets arranged at the corners of a square, not in a depression, each spinneret surrounded by a collar-like lamella. Anal valves (= paraprocts) simple, with margin expanded as narrow lips. Subanal scale (=

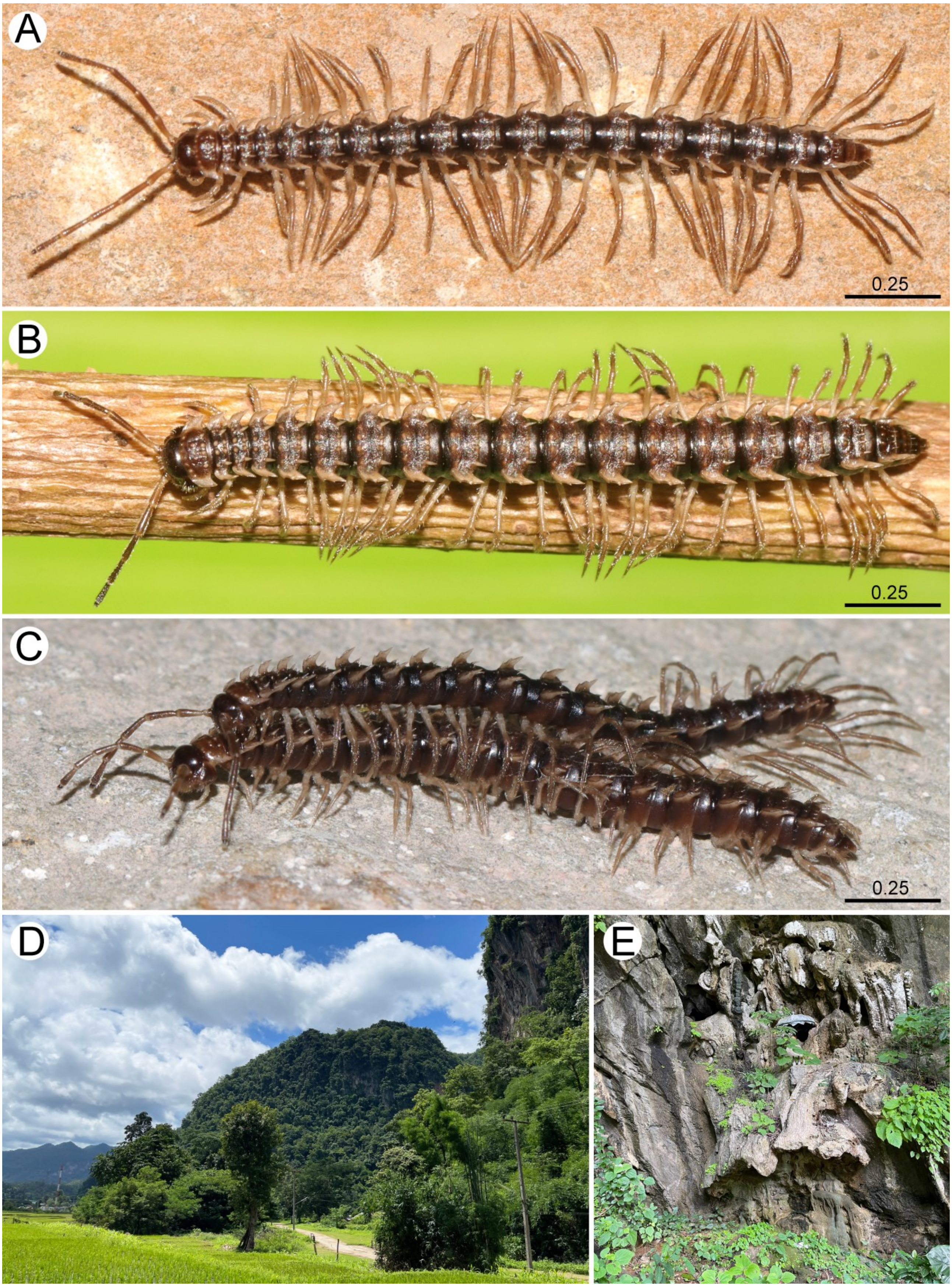

FIGURE 2. Photographs of live specimens and habitat of *Desmoxytes chaofa* sp. nov. (paratypes, MZKKU-MYR0014). (**A**) male paratype; (**B**) female paratype; (**C**) mating couple; (**D, E**) limestone habitat. Scale bars in centimetres.

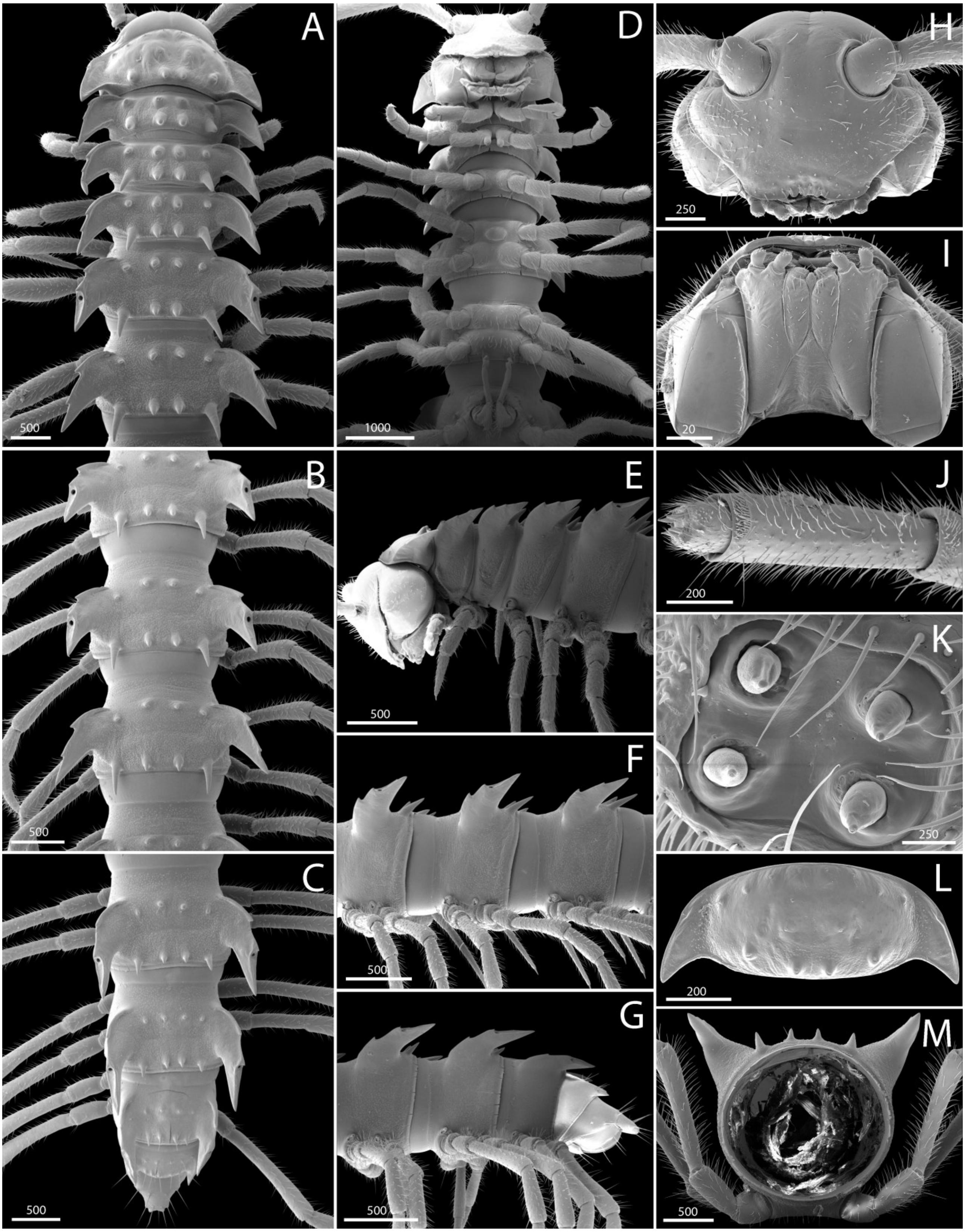

FIGURE 3. *Desmoxytes chaofa* sp. nov., male paratype (MZKKU-MYR0014) — SEM. (**A, D, E**) anterior body part, dorsal, ventral and lateral views, respectively; (**B, F**) body rings 9–11, dorsal and lateral views, respectively; (**C, G**) posterior body part and telson, dorsal and lateral views, respectively; (**H**) head, anterior view; (**I**) gnathochilarium, posterior view; (**J, K**) tip of antenna; (**L**) collum, dorsal view; (**M**) body ring 9, posterior view. Scale bars in micrometres.

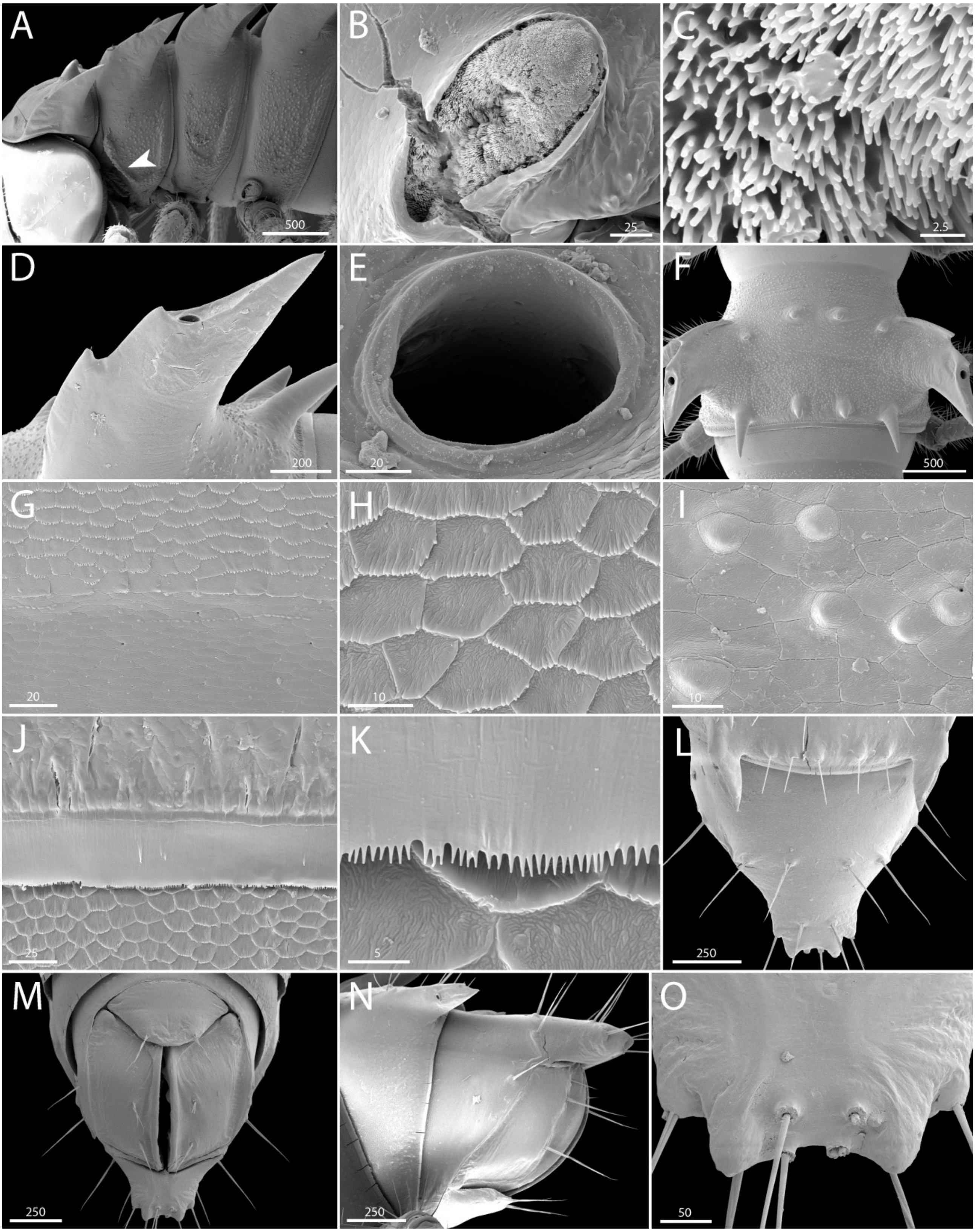

FIGURE 4. *Desmoxytes chaofa* sp. nov., male paratype (MZKKU-MYR0014) — SEM. (**A**) body rings 2–4, arrows points to pleurosternal keel on ring 2; (**B, C**) spiracle; (**D**) paratergum; (**E**) ozopore; (**F**) body ring 10; (**G**) stricture between prozonum and metazonum; (**H, I**) tegument of prozonum and metazonum, respectively; (**J, K**) limbus; (**L–N**) telson, dorsal, ventral and lateral views, respectively; (**O**) spinnerets. Scale bars in micrometres.

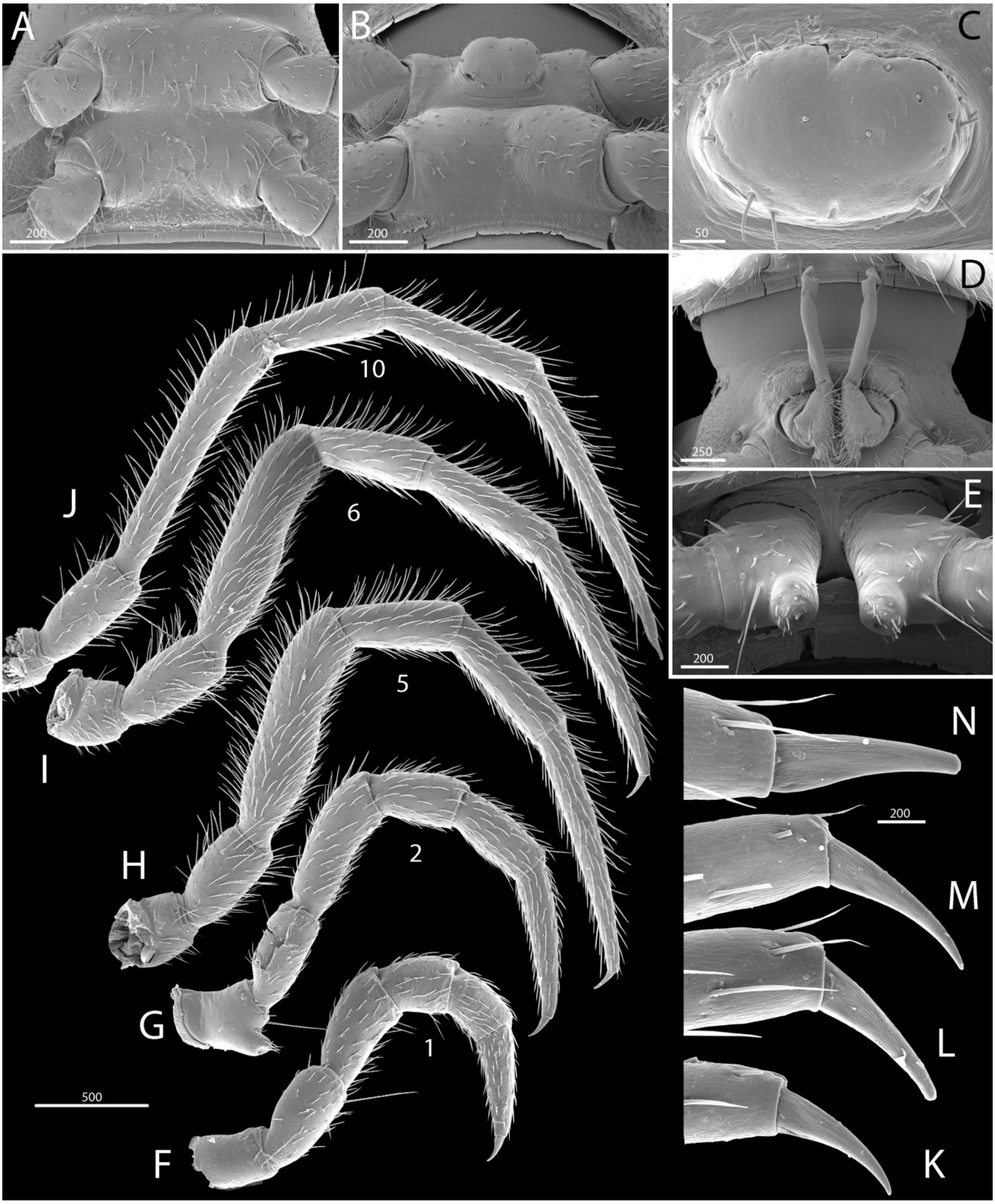

FIGURE 5. *Desmoxytes chaofa* sp. nov., male paratype (MZKKU-MYR0014) — SEM. (**A**) sternum 10; (**B**) sternum of ring 4; (**C**) sternal lobe between coxae 4; (**D**) gonopods; (**E**) gonopores on coxae 2; (**F**) leg 1; (**G**) leg 2; (**H**) leg 5; (**I**) leg 6; (**J**) leg 10; (**K**) claw of leg 2; (**L**) claw of leg 5; (**M**) claw of leg 6; (**N**) claw of leg 10. Scale bars in micrometres.

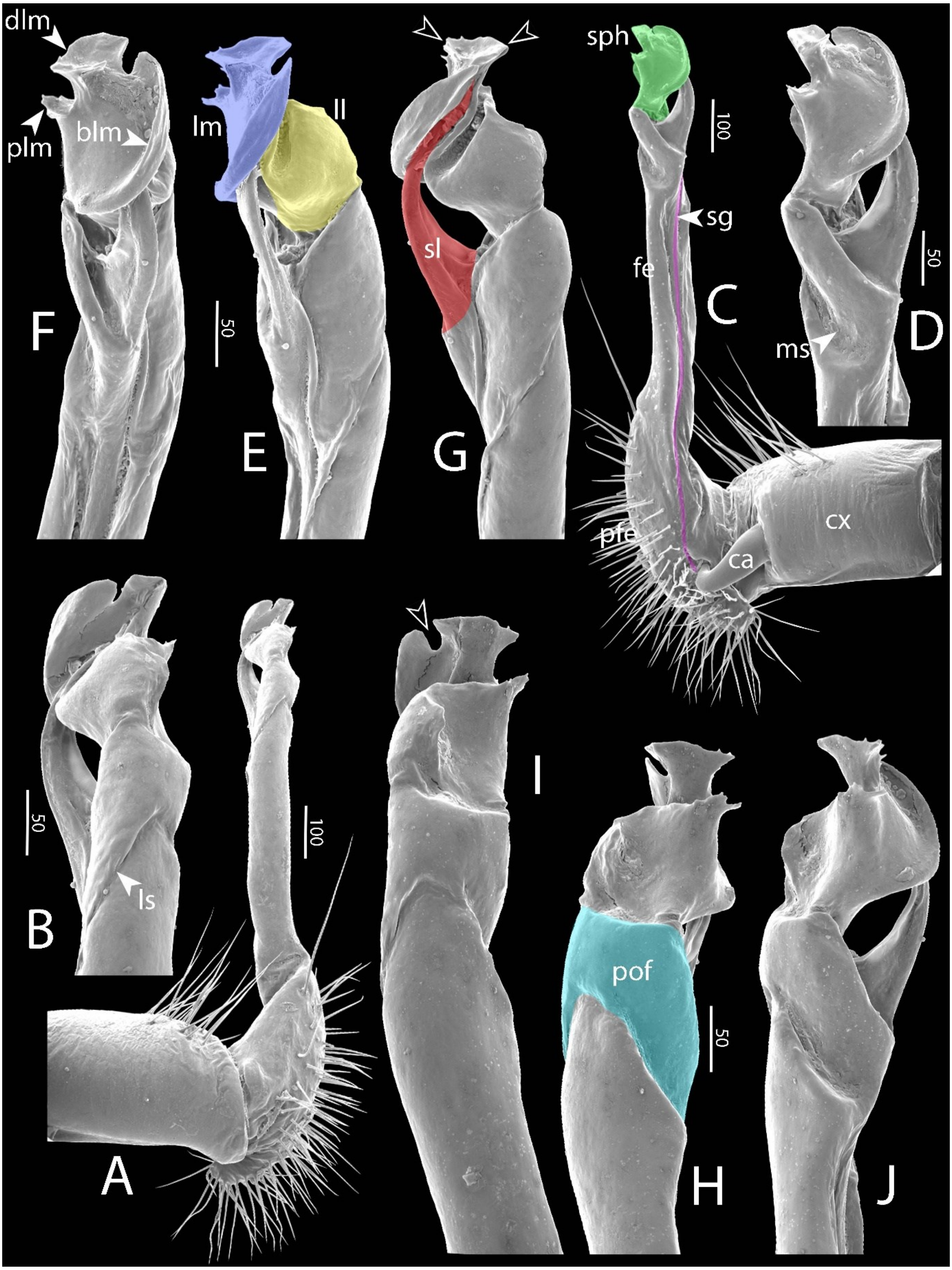

FIGURE 6. *Desmoxytes chaofa* sp. nov., male paratype (MZKKU-MYR0014) — SEM, right gonopod. (**A, B**) lateral view; (**C, D**) mesal view; (**E**) dorsal view; (**F, G**) subdorsal view; (**H**) ventral view; (**I, J**) subventral view. Black arrows on **G** = lamellae on dlm, black arrow on **I** = indentation demarcating dlm and blm. Abbreviations: blm = broad lobe of lamina medialis, cx = coxa, ca = cannula, dlm = distal lobe of lamina medialis, fe = femur, ll = lamina lateralis, lm = lamina medialis, ms = mesal sulcus, pfe = prefemur, plm = process on lamina medialis, pof = postfemoral part, sg = seminal groove, sl = solenomere, sph = solenophore. Scale bars in micrometres.

hypoproct) subtrapeziform, with inconspicuous setiferous tubercles at distal margin.

Sterna (Fig. 5A–C). Sparsely setose. Sternal lobe between male coxae 4 large, subtrapeziform; oval when seen in ventral view; tip round; with 2 conspicuous pores posteriorly.

Legs (Fig. 5E–N). Long and slender, ca. 3 times as long as body diameter. Male femora 5 and 6 modified, swollen ventrally. Tarsal brushes absent.

Gonopods (Figs 5D; 6). Coxa (cx) quite long, slightly longer than prefemur; surface smooth. Cannula (cx) slender. Prefemur (pfe) ca. 3/4 as long as femur. Femur (fe) long and slender. Mesal sulcus (ms) and lateral sulcus (ls) conspicuous, very deep and wide; clearly demarcating femur from postfemoral part. Postfemoral part (pof) conspicuous, slender. Solenophore (sph) well-developed, slender. Lamina lateralis (ll) conspicuous; swollen, lobelike; forming a thin and long ridge mesally, running parallel to solenomere. Lamina medialis (lm) well-developed. Process (plm) quite short; tip terminating in small branches; directed mesad. Distal lobe (dlm) well-developed, distally with two lamellae (lateral lamella broad and thin, projecting laterad; mesal lamella shorter than lateral one, apical margin serrate). Broad lobe (blm) thick, distinctly demarcated from distal lobe (dlm) by a very deep and narrow indentation. Solenomere (sl) quite short; protected by solenophore; tip not reaching over distal lobe of lamina medialis.

Remarks.– Srisonchai et al. (2018a) initially classified the bleached specimens collected from two locations in Mae Hong Son province as *D. planata* (Tham Pla-Namtok Pha Suea National Park and Tham Phadaeng, both relatively close to each other). However, following a thorough re-examination of these specimens, we have now re-identified them as representatives of this newly described species.

Distribution and habitat (Figs 2D, E; 12).– The newly discovered species has been documented exclusively at a few nearby locations, suggesting a highly limited distribution. It was observed moving along rock walls and appears to be restricted to humid limestone habitats. The rocky surfaces in this environment are covered with moisture-retaining mosses, while small herbaceous plants emerge from the crevices, possibly contributing to the overall damp microhabitat essential for the species' survival.

Desmoxytes sirindhornae **Srisonchai, sp. nov.**
https://zoobank.org/urn:lsid:zoobank.org:act: EA85B482-6358-4B4D-8E1C-7A7DCA675A2F
(Figs 7–11)

Material examined.– Holotype: Male (MZKKU) THAILAND, Tak Province, Tha Song Yang District, Nam Ok Ru Monastery, 17°31'40.2"N 97°57'48.9"E, ca. 120 m a.s.l., coll. R. Srisonchai, K. Srikampha and T. Benchapong, 11 August 2024. Paratypes: 40 males, 33 females (MZKKU), same data as holotype. 1 male, 1 female (CUMZ), same data as holotype. 1 male, 1 female (NHMD), same data as holotype. 1 male, 1 female (NHMUK), same data as holotype. 1 male, 1 female (NHMW), same data as holotype. 1 male, 1 female (ZFMK), same data as holotype.

Etymology.– This species is named in honour of Her Royal Highness Princess Maha Chakri Sirindhorn, whose remarkable contributions have significantly advanced biodiversity research and the preservation of Thailand's natural heritage for future generations. Her unwavering commitment continues to inspire scientists, conservationists, and the public in efforts to safeguard the nation's ecosystems. She has played a pivotal role in fostering scientific collaborations, supporting research institutions, and encouraging young scholars to pursue ecological and environmental studies. Her dedication spans a wide range of conservation initiatives, including the protection of endangered species, forest conservation, and the promotion of sustainable resource management.

Diagnosis.– Brownish pink/pink paraterga in contrast with brown body colour, metaterga 2–19 with 2+2 setiferous tubercles in both anterior and posterior rows, hypoproct apically concave or truncate. Similar in these respects to *D. des*, but differs from this species by the combination of these characters: paraterga more slender (*vs* broad, cleaverlike), sternal lobe between male coxa 4 flattened (*vs* oval and stout), mesal sulcus shallow (*vs* very deep), lateral sulcus deep and narrow (*vs* inconspicuous), lamina lateralis without a distinct sulcus apically (*vs* with a sulcus dividing into two main ridges), process of lamina medialis long (*vs* short), distal lobe and broad lobe of lamina medialis clearly demarcated by indentation (*vs* no demarcation).

Description.–

Size (Fig. 7A–C). Length 22–26 mm (male), 25–33 mm (female); width of midbody metazona ca. 1.2 mm (male), ca. 1.4 mm (female). Width of head < collum = ring 2 = 3 = 4 < 5–17, thereafter body gradually tapering towards telson.

Colour (Fig. 7A–C). Specimens in life with black body in contrast to pink paraterga; head, prozona, metaterga, base of paraterga, surface below paraterga, telson and sterna black; antenna dark brown (except

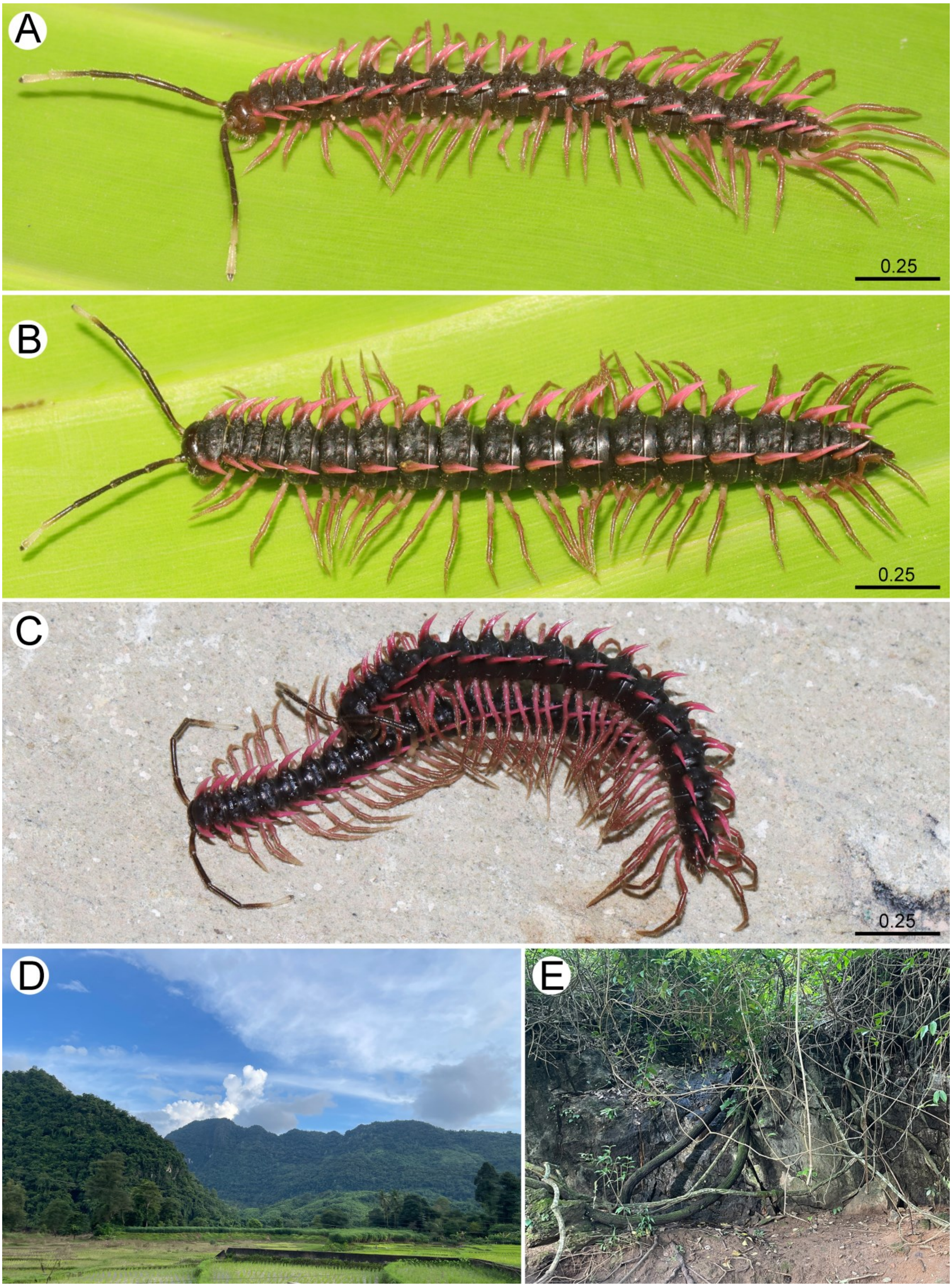

FIGURE 7. Photographs of live specimens and habitat of *Desmoxytes sirindhornae* sp. nov. (paratypes, MZKKU-MYR0016). (**A**) male paratype (**B**) female paratype (**C**) amorous couple of adults (**D, E**) limestone habitat. Scale bars in centimetres.

brownish white antennomeres 5 and 6); epiproct and legs pinkish brown.

Head and mouthparts (Figs 7A–C; 8E, H, I). Vertex bare. Epicranial suture conspicuous on vertex. Labrum and clypeus sparsely setose. Mouthparts as typical in paradoxosomatids, not dissected.

Antennae (Figs 7A–C; 8J, K). Very long and slender, reaching backward to ring 6–7 in male and 5–6 in female when stretched dorsally; antennomeres 5–7 with short sensilla near distal part; antennomere 8 with four conical sensilla.

Collum (Figs 8E, L; 9A). With 3+3 setiferous tubercles in anterior row, 1+1 setiferous tubercles in intermediate row and 2+2 setiferous tubercles in posterior row. Paraterga of collum elevated at about 30°, directed caudolaterad; lateral margin with two inconspicuous setiferous notches on each side; tip sharp.

Tegument (Figs 9F–I; 10A, D). Prozona finely shagreened. Metaterga, base of paraterga and surface below paraterga with microgranulations. Laterally with small wrinkles below base of paraterga. Paraterga, sterna and telson smooth.

Spiracles (Fig. 9B, C). Ovoid; with small spiracular filters, brush border-like.

Metaterga (Figs 8A–C; 9F). Metaterga 2–19 with 2+2 conspicuous setiferous tubercles in anterior row and 2+2 setiferous tubercles in posterior row. Tubercles in posterior row larger than those in anterior one. Suture between prozona and metazona shallow and wide. Axial line absent. Suture on metaterga shallow and wide, conspicuous on rings 2–17.

Limbus of midbody ring (Fig. 9J, K). Conspicuous; with rows of very long filaments, fused together and forming an anteroposteriorly striate; margin finely spiculate, spicules unequal in size.

Paraterga (Figs 8A–C, E–G, M; 9D, E). Paraterga of rings 2–18 strongly developed, winglike; Paraterga of rings 18–19 gradually tapering towards telson. Elevated at about 60° (male) and 50° (female); directed caudolaterad (except in rings 17–19 directed more caudad); lateral margin with two conspicuous setiferous notches; on pore-bearing rings sometimes with a tiny notch located close to the tip; tip acute. Ozopore conspicuous, oval, located at about half of midbody height of paraterga.

Pleurosternal keel (Fig. 9A). Conspicuous, simple long ridge on ring 2; small ridge on ring 3; thereafter missing.

Telson (Fig. 9L–O). Preanal ring with conspicuous conical epiproct, quite short; lateral setiferous tubercles stout and short; apical tubercles conspicuous, lobelike; tip concave; spinnerets arranged at the corners of a square, not in a depression, each spinneret surrounded by a collar-like lamellae. Anal valves (= paraprocts) regular, with margin extended as narrow lips. Subanal scale (= hypoproct) trapeziform, with inconspicuous setiferous tubercles at distal margin.

Sterna (Fig. 10A–D). Sparsely setose. Sternal lobe between male coxae 4 conspicuous, flattened anteroposteriorly, subsemicircular when seen in posterior view; tip subtruncate; with 2 conspicuous pores posteriorly.

Legs (Fig. 10F–M). Long and slender, ca. 3 times as long as body diameter. Male femora 5 and 6 modified, swollen ventrally. Tarsal brushes absent.

Gonopods (Figs. 10E; 11). Coxa (cx) quite long, longer than prefemur, equal in length to femur; surface smooth. Cannula (cx) slender and curved distally, swollen at base. Prefemur (pfe) ca. 3/4 as long as femur. Femur (fe) straight and slender. Mesal sulcus (ms) conspicuous, deep and wide. Lateral sulcus (ls) very deep and narrow. Postfemoral part (pof) conspicuous; wide in lateral view; narrow in mesal view. Solenophore (sph) well-developed, quite compact and slightly stout. Lamina lateralis (ll) conspicuous; swollen, lobelike; mesally forming a thin and long ridge, running parallel to solenomere. Lamina medialis (lm) well-developed. Process (plm) quite long; tip blunt; directed mesolaterad. Distal lobe (dlm) with one conspicuous lamella distally; tip directed lateroventrad. Broad lobe (blm) thick, distinctly demarcated from distal lobe (dlm) by a deep and narrow indentation. Solenomere (sl) quite short; protected by solenophore; tip not reaching over distal lobe.

Remarks.– In overall appearance, the new species is easily distinguishable from all other *Desmoxytes* species by its long, bright pink paraterga contrasting with a black body, along with the presence of small tubercles on the metaterga. No variation has been observed.

Distribution and habitat (Figs 7D, E; 12).– This species is known only from the type locality. All specimens were observed crawling on rock walls or large limestone boulders with moist surfaces. No specimens were found on the ground or on tree branches, which may indicate a specific habitat preference for this species.

DISCUSSION

Desmoxytes chaofa sp. nov. and *D. sirindhornae* sp. nov. are taxonomically assigned to the genus *Desmoxytes* based on the following morphological characteristics: (1) wing-like paraterga, (2) metaterga bearing two rows of tubercles, cones, or spines, (3) modifications in the male leg femora, and (4) a

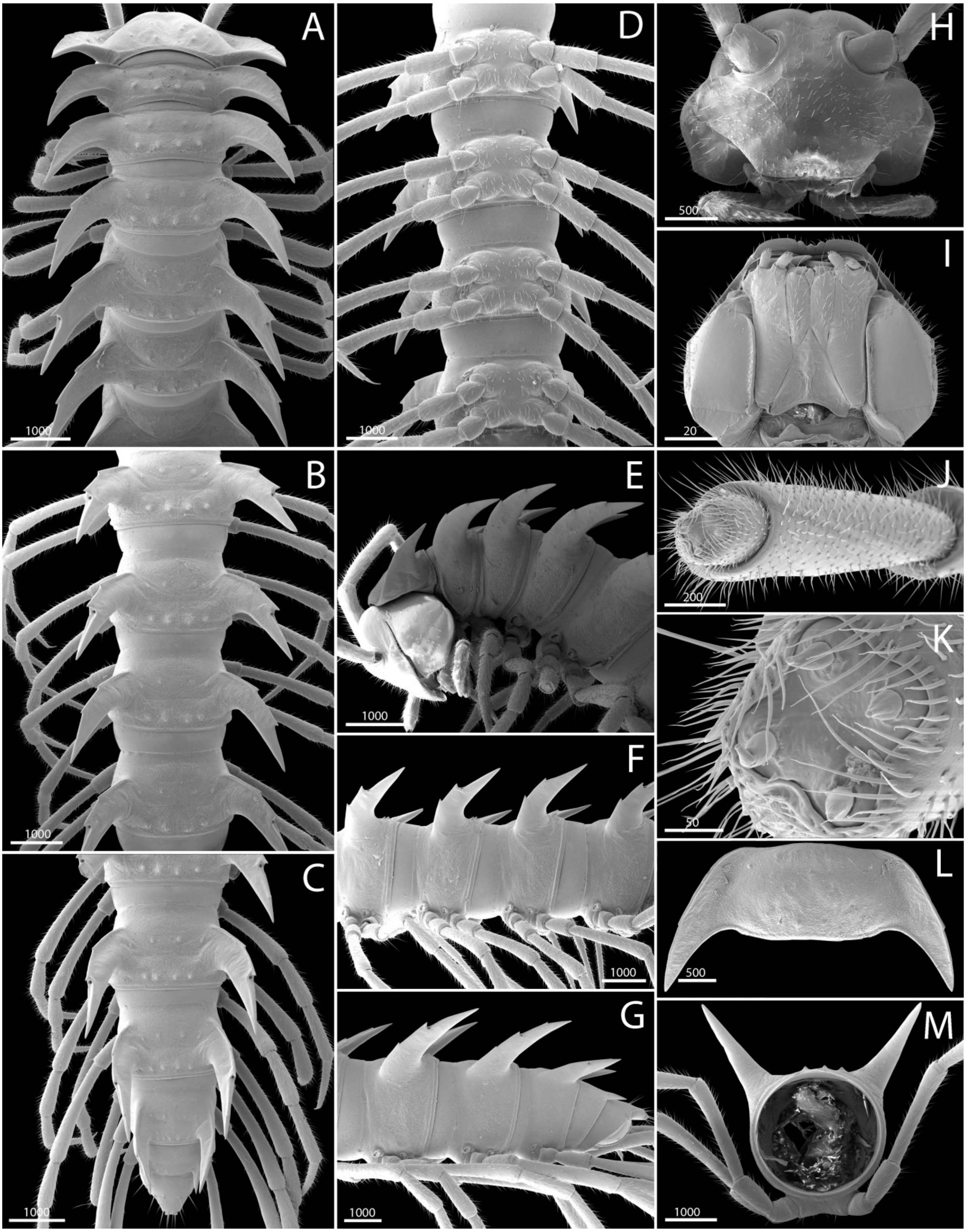

FIGURE 8. *Desmoxytes sirindhornae* sp. nov., male paratype (MZKKU-MYR0016) — SEM. (**A, D, E**) anterior body part, dorsal ventral and lateral views, respectively; (**B, F**) body rings 9–11, dorsal and lateral views, respectively; (**C, G**) posterior body part and telson, dorsal and lateral views, respectively; (**H**) head, anterior view; (**I**) gnathochilarium, posterior view; (**J, K**) tip of antenna; (**L**) collum, dorsal view; (**M**) body ring 9, posterior view. Abbreviations: (gs = gnathochilarial stipes, I = lingual lobe, me = mentum) Scale bars in micrometres.

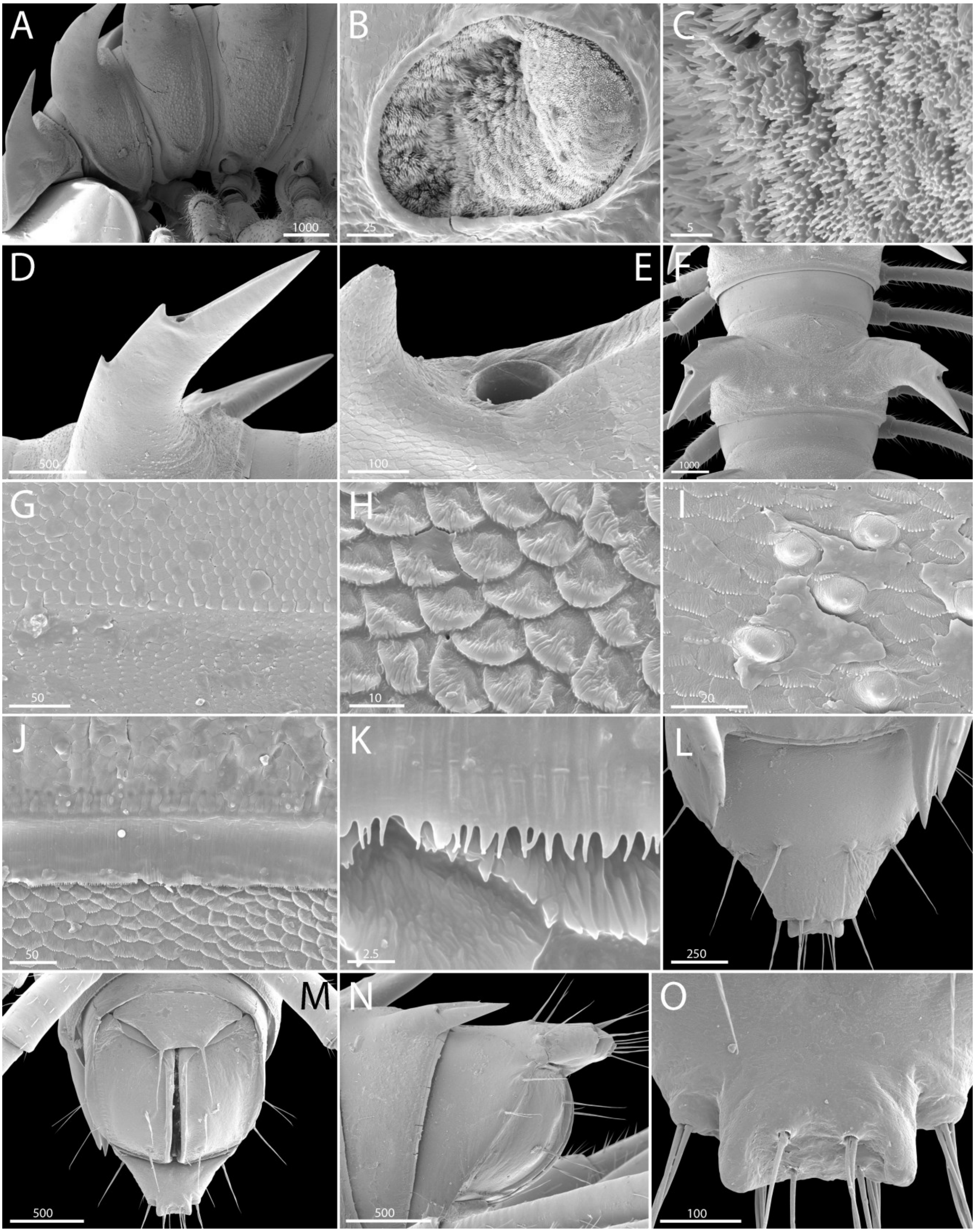

FIGURE 9. *Desmoxytes chaofa* sp. nov., male paratype (MZKKU-MYR0016) — SEM. (**A**) body rings 2–4, arrows points to pleurosternal keel on ring 2; (**B, C**) spiracle; (**D**) paratergum; (**E**) ozopore; (**F**) body ring 10; (**G**) stricture between prozonum and metazonum; (**H, I**) tegument of prozonum and metazonum, respectively; (**J, K**) limbus; (**L–N**) telson, dorsal, ventral and lateral views, respectively; (**O**) spinnerets. Scale bars in micrometres.

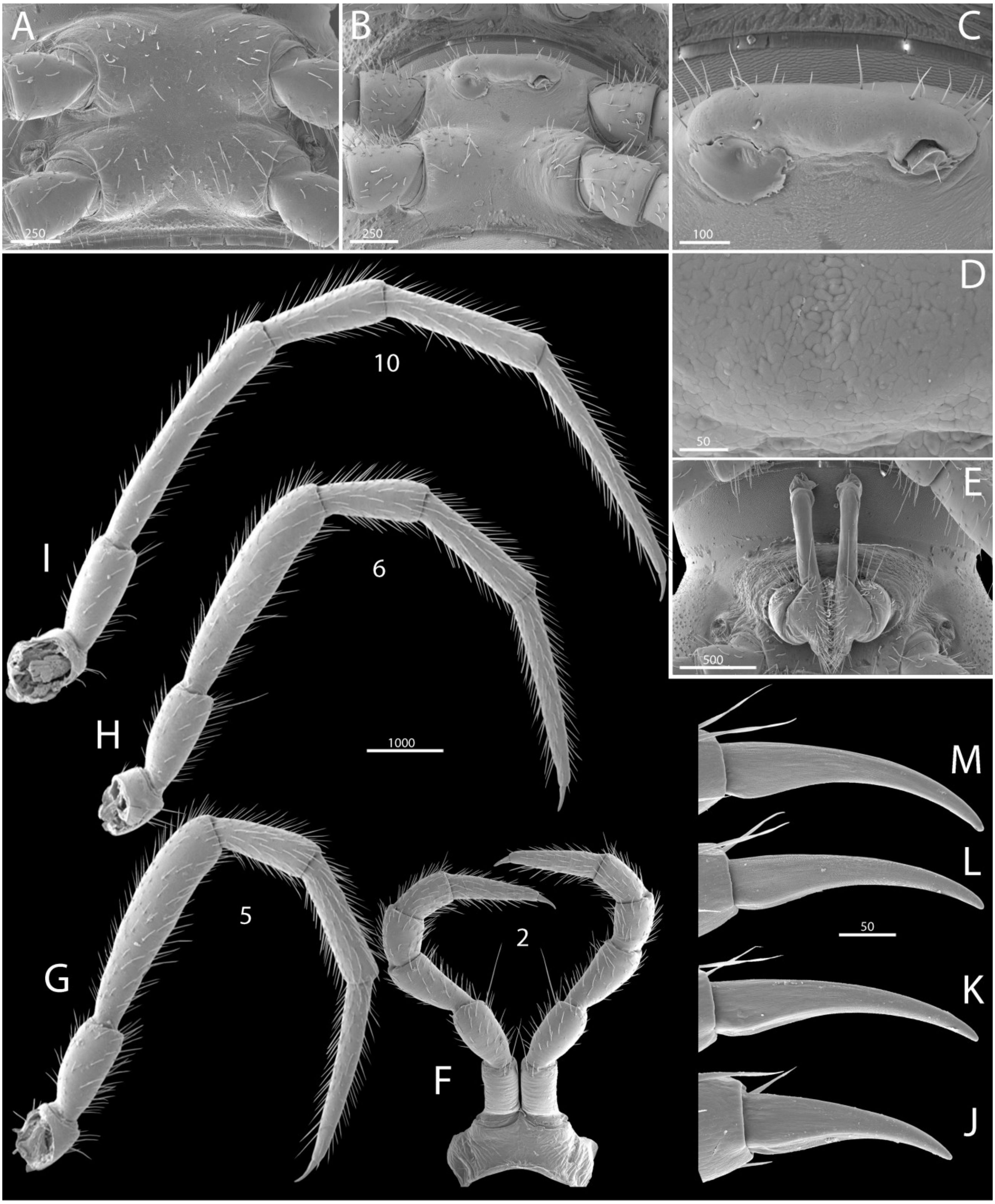

FIGURE 10. *Desmoxytes sirindhornae* sp. nov., male paratype (MZKKU-MYR0016) — SEM. (**A**) sternum 10; (**B**) sternum of ring 4; (**C**) sternal lobe between coxae 4; (**D**) surface of sternal lobe between coxae 4; (**E**) gonopods; (**F**) leg pair 2; (**G**) leg 5; (**H**) leg 6; (**I**) leg 10; (**K**) claw of leg 2; (**L**) claw of leg 5; (**M**) claw of leg 6; (**N**) claw of leg 10. Scale bars in micrometres.

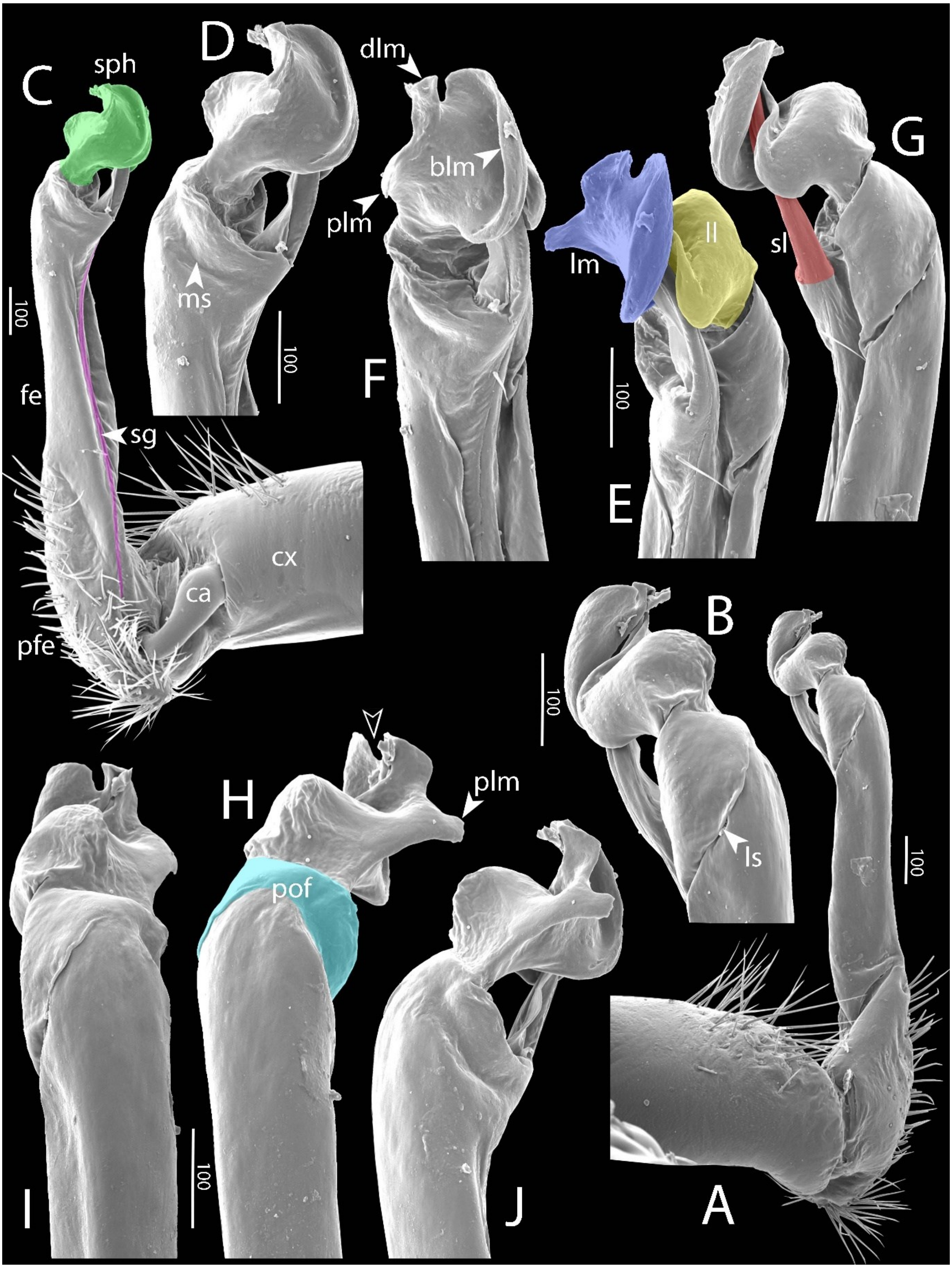

FIGURE 11. *Desmoxytes sirindhornae* sp. nov., male paratype (MZKKU-MYR0016) — SEM, right gonopod. (**A, B**) lateral view; (**C, D**) mesal view; (**E**) dorsal view; (**F, G**) subdorsal view; (**H**) ventral view; (**I, J**) subventral view. Black arrows on H = indentation demarcating dlm and blm. Abbreviations: blm = broad lobe of lamina medialis, cx= coxa, ca = cannula, dlm = distal lobe of lamina medialis, fe = femur, ll = lamina lateralis, lm = lamina medialis, ms = mesal sulcus, pfe = prefemur, plm = process on lamina medialis, pof = postfemoral part, sg = seminal groove, sl = solenomere, sph = solenophore. Scale bars in micrometres.

gonopod telopodite with a distinct postfemoral part and a lamina lateralis clearly demarcated from lamina medialis. These two species can be easily distinguished from all other *Desmoxytes* congeners by their unique body colouration and specific details of the gonopod telopodite. Details of gonopod morphology continues to provide a reliable criteria for species delimitation (Likhitrakarn et al., 2011; Decker, 2016a, 2016b; Means et al., 2021a, 2021b). Additionally, the genetic data incorporating three gene markers (COI, 16S rRNA, and 28S rRNA) support the recognition of these two new species. The mean interspecific divergence in COI sequences compared to congeners was 14.72% for *D. chaofa* sp. nov. and 13.04% for *D. sirindhornae* sp. nov. These values fall within the range of interspecific genetic distances observed in other dragon millipede genera, which have an average of approximately 13.72% (Nguyen et al., 2019; Srisonchai et al., 2024).

A multi-locus phylogenetic analysis confirmed that all members of *Desmoxytes* form a monophyletic group with strong statistical support in both Bayesian inference (BI) and maximum likelihood (ML) analyses (Fig. 1). This finding clearly validates the placement of the two newly described species within this genus. Additionally, the phylogenetic tree indicates that each new species clusters with their morphologically most similar species. *Desmoxytes chaofa* sp. nov. groups with *D. octoconigera* – both these share a dark brown body colouration and a similarly slender distal part of the gonopod. Meanwhile, *D. sirindhornae* sp. nov. is grouped together with *D. des* – both share pink paraterga, a brown body, and metatergal tubercle pattern of 2+2 on rings 2–19. Beyond the scope of this study, both BI and ML trees (Fig. 1) suggested that the phylogenetic positions of nearly all species-level clades are well supported (PP = 0.89–1.00 and BS = 100). While the BI tree resolves in most deep nodes, the ML analysis provides slightly different results with lower support (see Fig. 1 and Fig. A1). These differences can be attributed to the inherent differences between the Bayesian and ML methods, including the use of posterior probabilities vs. bootstrapping for node support and differences in the underlying statistical models (Erixon et al., 2003). Furthermore, the use of only three gene markers (COI, 16S rRNA, 28S rRNA) may provide limited phylogenetic signal, especially at deeper nodes. To achieve a more robust phylogenetic resolution, future studies should incorporate additional genetic markers, such as ND1, histone 3, 18S rRNA, ITS, or employ complete mitochondrial/whole genomes (Means et al., 2021b; Zuo et al., 2022).

All specimens of the newly discovered species were found exclusively on limestone rock walls or within crevices, requiring collectors to climb in order to retrieve specimens. This habitat preference is reminiscent of the genus *Spinaxytes*, which similarly occupies specialized limestone microhabitats (Srisonchai et al., 2018d). Notably, *D. chaofa* sp. nov. shows a dark body colouration that allows it to blend visually with the brown or black humid rocks, which may contribute to concealment in its habitat. Both *D. sirindhornae* sp. nov. and *D. chaofa* sp. nov. are distributed along a limestone range near the Myanmar border, suggesting the potential for their occurrence in adjacent regions of Myanmar. From a biogeographic perspective, these newly discovered species have been recorded only at their type locality or within closely restricted areas, leading us to consider them endemic to northern Thailand. This pattern aligns with the known distribution of other limestone-adapted millipede taxa, including all described genera of dragon millipedes in Thailand (Enghoff et al., 2007; Likhitrakarn et al., 2024; Srisonchai et al., 2016; 2018a, 2018b, 2018c, 2018d, 2020, 2024). Since the discovery of the famous shocking pink species (*D. purpurosea*) in 2007, intensive surveys of Thai millipedes have yielded numerous new genera and species, expanding the total number of *Desmoxytes* species to 20. Given the species diversity and endemism of limestone-adapted millipedes, further field studies in karsts may reveal additional *Desmoxytes* species across Thailand.

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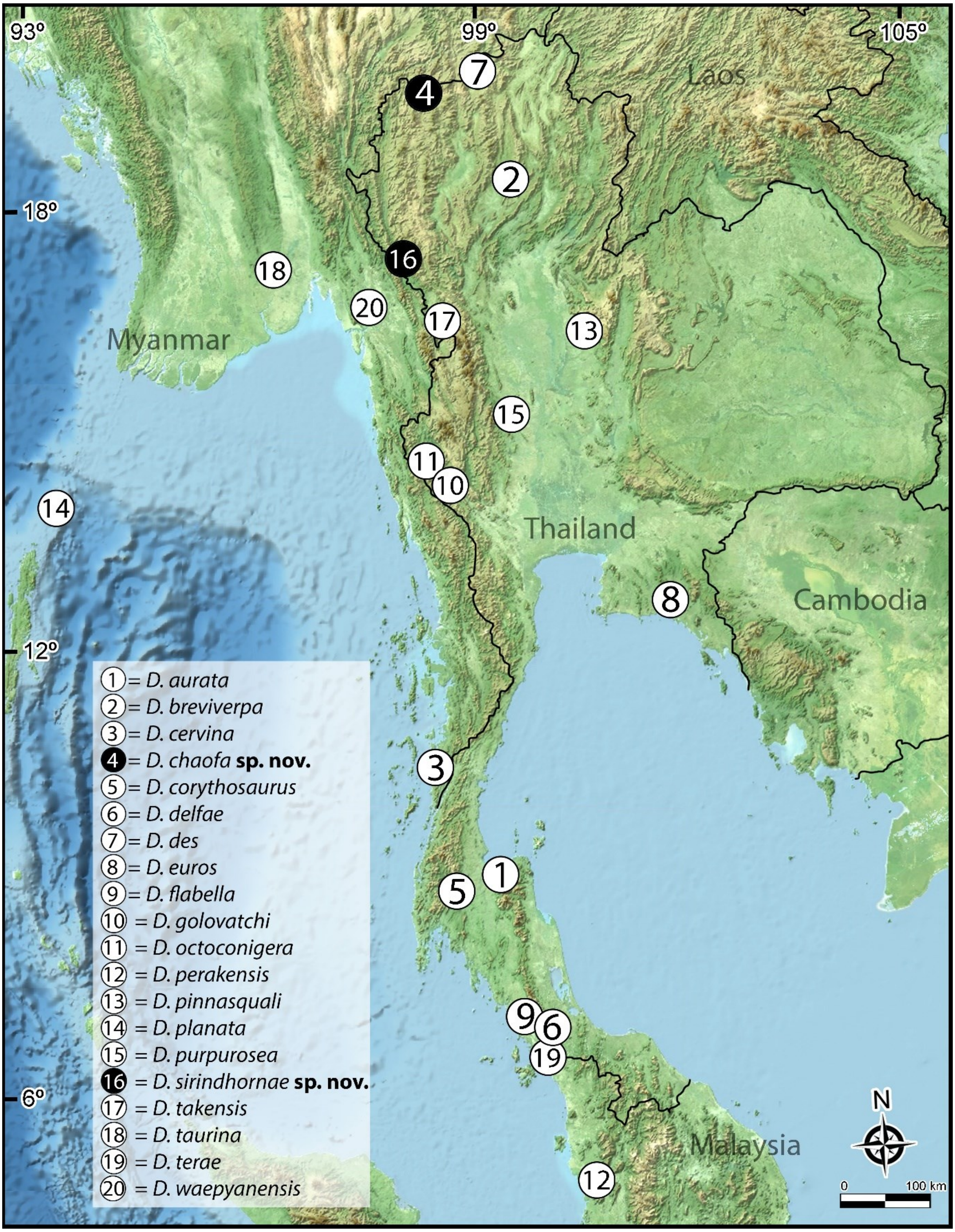

FIGURE 12. Distribution map of type locality of all *Desmoxytes* species.

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APPENDIX

TABLE A1. Genetic distance of COI gene.

	Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	*Desmoxytes aurata* (095)															
2	*Desmoxytes aurata* (096)	0.0048														
3	*Desmoxytes breviverpa* (048)	0.1335	0.1336													
4	*Desmoxytes breviverpa* (053)	0.1335	0.1336	0.0000												
5	*Desmoxytes cervina* (B4)	0.1503	0.1487	0.1325	0.1325											
6	*Desmoxytes cervina* (B6)	0.1503	0.1487	0.1325	0.1325	0.0000										
7	*Desmoxytes cervina* (B7)	0.1503	0.1487	0.1344	0.1344	0.0063	0.0063									
8	*Desmoxytes cervina* (K2)	0.1063	0.1065	0.1169	0.1169	0.0901	0.0901	0.0897								
9	*Desmoxytes chaofa* sp. nov. (KS164)	0.1380	0.1374	0.1564	0.1564	0.1867	0.1867	0.1867	0.1212							
10	*Desmoxytes chaofa* sp. nov. (KS165)	0.1380	0.1374	0.1564	0.1564	0.1867	0.1867	0.1867	0.1212	0.0000						
11	*Desmoxytes chaofa* sp. nov. (KS167)	0.1380	0.1374	0.1564	0.1564	0.1867	0.1867	0.1867	0.1212	0.0000	0.0000					
12	*Desmoxytes chaofa* sp. nov. (KS168)	0.1380	0.1374	0.1564	0.1564	0.1867	0.1867	0.1867	0.1212	0.0000	0.0000	0.0000				
13	*Desmoxytes chaofa* sp. nov. (KS169)	0.1380	0.1374	0.1564	0.1564	0.1867	0.1867	0.1867	0.1212	0.0000	0.0000	0.0000	0.0000			
14	*Desmoxytes corythosaurus* (017)	0.1549	0.1551	0.1183	0.1183	0.1021	0.1021	0.1037	0.1284	0.1256	0.1256	0.1256	0.1256	0.1256		
15	*Desmoxytes delfae* (M2)	0.0955	0.0958	0.1003	0.1003	0.1580	0.1580	0.1577	0.1152	0.1435	0.1435	0.1435	0.1435	0.1435	0.1547	
16	*Desmoxytes delfae* (M3)	0.0875	0.0878	0.0987	0.0987	0.1544	0.1544	0.1542	0.1143	0.1452	0.1452	0.1452	0.1452	0.1452	0.1442	0.0101
17	*Desmoxytes des* (DAK)	0.1569	0.1558	0.0952	0.0952	0.1252	0.1252	0.1246	0.1071	0.1169	0.1169	0.1169	0.1169	0.1169	0.1180	0.1144
18	*Desmoxytes des* (KS154)	0.1232	0.1226	0.0892	0.0892	0.1423	0.1423	0.1423	0.1012	0.1067	0.1067	0.1067	0.1067	0.1067	0.1203	0.1168
19	*Desmoxytes des* (KS156)	0.1232	0.1226	0.0892	0.0892	0.1423	0.1423	0.1423	0.1012	0.1067	0.1067	0.1067	0.1067	0.1067	0.1203	0.1168
20	*Desmoxytes euros* (160)	0.1771	0.1774	0.1503	0.1503	0.2026	0.2026	0.2029	0.1787	0.1297	0.1297	0.1297	0.1297	0.1297	0.1462	0.1707
21	*Desmoxytes euros* (161)	0.1783	0.1786	0.1513	0.1513	0.2033	0.2033	0.2036	0.1801	0.1299	0.1299	0.1299	0.1299	0.1299	0.1474	0.1707
22	*Desmoxytes flabella* (212)	0.0971	0.0973	0.1263	0.1263	0.1751	0.1751	0.1708	0.0887	0.1660	0.1660	0.1660	0.1660	0.1660	0.1542	0.1046
23	*Desmoxytes flabella* (213)	0.0971	0.0973	0.1263	0.1263	0.1751	0.1751	0.1708	0.0887	0.1660	0.1660	0.1660	0.1660	0.1660	0.1542	0.1046
24	*Desmoxytes golovatchi* (A4)	0.1275	0.1275	0.0679	0.0679	0.1226	0.1226	0.1253	0.1105	0.1282	0.1282	0.1282	0.1282	0.1282	0.1229	0.1201
25	*Desmoxytes golovatchi* (B15)	0.1317	0.1317	0.0690	0.0690	0.1271	0.1271	0.1300	0.1145	0.1319	0.1319	0.1319	0.1319	0.1319	0.1318	0.1212
26	*Desmoxytes octoconigera* (A10)	0.1673	0.1653	0.1284	0.1284	0.1181	0.1181	0.1192	0.1143	0.1350	0.1350	0.1350	0.1350	0.1350	0.1341	0.1360
27	*Desmoxytes octoconigera* (A11)	0.1689	0.1669	0.1299	0.1299	0.1181	0.1181	0.1189	0.1169	0.1345	0.1345	0.1345	0.1345	0.1345	0.1368	0.1381
28	*Desmoxytes pinnasquali* (055)	0.1621	0.1619	0.0807	0.0807	0.1382	0.1382	0.1402	0.1266	0.1502	0.1502	0.1502	0.1502	0.1502	0.1138	0.1118
29	*Desmoxytes pinnasquali* (059)	0.1621	0.1619	0.0807	0.0807	0.1382	0.1382	0.1402	0.1266	0.1502	0.1502	0.1502	0.1502	0.1502	0.1138	0.1118
30	*Desmoxytes pinnasquali* (KS188)	0.1562	0.1561	0.0816	0.0816	0.1423	0.1423	0.1439	0.1217	0.1572	0.1572	0.1572	0.1572	0.1572	0.1149	0.1107
31	*Desmoxytes pinnasquali* (KS189)	0.1562	0.1561	0.0816	0.0816	0.1423	0.1423	0.1439	0.1217	0.1572	0.1572	0.1572	0.1572	0.1572	0.1149	0.1107
32	*Desmoxytes purpurosea* (002)	0.1607	0.1613	0.1172	0.1172	0.1570	0.1570	0.1600	0.1515	0.1427	0.1427	0.1427	0.1427	0.1427	0.1253	0.1518
33	*Desmoxytes purpurosea* (159)	0.1654	0.1665	0.1348	0.1348	0.1669	0.1669	0.1664	0.1522	0.1205	0.1205	0.1205	0.1205	0.1205	0.1392	0.1433
34	*Desmoxytes purpurosea* (A22)	0.1612	0.1618	0.1148	0.1148	0.1580	0.1580	0.1608	0.1507	0.1443	0.1443	0.1443	0.1443	0.1443	0.1255	0.1514
35	*Desmoxytes purpurosea* (119)	0.1581	0.1580	0.0567	0.0567	0.1355	0.1355	0.1375	0.1010	0.1631	0.1631	0.1631	0.1631	0.1631	0.1155	0.1153
36	*Desmoxytes purpurosea* (120)	0.1581	0.1580	0.0567	0.0567	0.1355	0.1355	0.1375	0.1010	0.1631	0.1631	0.1631	0.1631	0.1631	0.1155	0.1153
37	*Desmoxytes purpurosea* (126)	0.1581	0.1580	0.0612	0.0612	0.1462	0.1462	0.1484	0.0998	0.1542	0.1542	0.1542	0.1542	0.1542	0.1127	0.1153
38	*Desmoxytes sirindhornae* sp. nov. (KS159)	0.1357	0.1353	0.1114	0.1114	0.1251	0.1251	0.1251	0.1097	0.1674	0.1674	0.1674	0.1674	0.1674	0.1306	0.1136
39	*Desmoxytes sirindhornae* sp. nov. (KS160)	0.1357	0.1353	0.1114	0.1114	0.1251	0.1251	0.1251	0.1097	0.1674	0.1674	0.1674	0.1674	0.1674	0.1306	0.1136
40	*Desmoxytes sirindhornae* sp. nov. (KS161)	0.1357	0.1353	0.1114	0.1114	0.1251	0.1251	0.1251	0.1097	0.1674	0.1674	0.1674	0.1674	0.1674	0.1306	0.1136
41	*Desmoxytes sirindhornae* sp. nov. (KS162)	0.1357	0.1353	0.1114	0.1114	0.1251	0.1251	0.1251	0.1097	0.1674	0.1674	0.1674	0.1674	0.1674	0.1306	0.1136
42	*Desmoxytes takensis* (063)	0.1230	0.1233	0.0367	0.0367	0.1257	0.1257	0.1268	0.0939	0.1409	0.1409	0.1409	0.1409	0.1409	0.1111	0.1006
43	*Desmoxytes takensis* (064)	0.1230	0.1233	0.0367	0.0367	0.1257	0.1257	0.1268	0.0939	0.1409	0.1409	0.1409	0.1409	0.1409	0.1111	0.1006
44	*Desmoxytes takensis* (136)	0.1208	0.1212	0.0323	0.0323	0.1271	0.1271	0.1286	0.0937	0.1623	0.1623	0.1623	0.1623	0.1623	0.1059	0.0891
45	*Desmoxytes terae* (220)	0.1057	0.1056	0.0905	0.0905	0.1796	0.1796	0.1835	0.0981	0.1460	0.1460	0.1460	0.1460	0.1460	0.1311	0.1116
46	*Desmoxytes terae* (M9)	0.1057	0.1056	0.0905	0.0905	0.1796	0.1796	0.1835	0.0981	0.1460	0.1460	0.1460	0.1460	0.1460	0.1311	0.1116
47	*Desmoxytes waepyanensis* (143)	0.1228	0.1232	0.0416	0.0416	0.1343	0.1343	0.1360	0.1139	0.1431	0.1431	0.1431	0.1431	0.1431	0.1278	0.1073
48	*Desmoxytes waepyanensis* (144)	0.1238	0.1242	0.0427	0.0427	0.1343	0.1343	0.1360	0.1151	0.1433	0.1433	0.1433	0.1433	0.1433	0.1276	0.1074
49	*Gigaxytes gigas* (K1)	0.1708	0.1697	0.1459	0.1459	0.1626	0.1626	0.1608	0.1860	0.1942	0.1942	0.1942	0.1942	0.1942	0.1626	0.1675
50	*Hylomus rhinoceros* (E12)	0.1934	0.1922	0.1371	0.1371	0.1760	0.1760	0.1760	0.1525	0.1574	0.1574	0.1574	0.1574	0.1574	0.1085	0.1263
51	*Nagaxytes erecta* (C7)	0.1456	0.1458	0.1636	0.1636	0.1757	0.1757	0.1728	0.1381	0.2310	0.2310	0.2310	0.2310	0.2310	0.1574	0.1786
52	*Orthomorpha* cf. *pterygota* (K9)	0.1541	0.1533	0.1510	0.1510	0.1953	0.1953	0.1953	0.1583	0.1613	0.1613	0.1613	0.1613	0.1613	0.1732	0.1547
53	*Pogonosternum adrianae*	0.2217	0.2208	0.1694	0.1694	0.1934	0.1934	0.1934	0.1868	0.1684	0.1684	0.1684	0.1684	0.1684	0.1140	0.2385
54	*Pogonosternum laetificum*	0.2283	0.2276	0.1474	0.1474	0.2427	0.2427	0.2427	0.2016	0.2124	0.2124	0.2124	0.2124	0.2124	0.1082	0.2157
55	*Siamaxytes bifurca* (C14)	0.1413	0.1418	0.1343	0.1343	0.1700	0.1700	0.1683	0.1671	0.1403	0.1403	0.1403	0.1403	0.1403	0.1635	0.0960

APPENDIX

TABLE A1. Continued.

	Taxa	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1	*Desmoxytes aurata* (095)															
2	*Desmoxytes aurata* (096)															
3	*Desmoxytes breviverpa* (048)															
4	*Desmoxytes breviverpa* (053)															
5	*Desmoxytes cervina* (B4)															
6	*Desmoxytes cervina* (B6)															
7	*Desmoxytes cervina* (B7)															
8	*Desmoxytes cervina* (K2)															
9	*Desmoxytes chaofa* sp. nov. (KS164)															
10	*Desmoxytes chaofa* sp. nov. (KS165)															
11	*Desmoxytes chaofa* sp. nov. (KS167)															
12	*Desmoxytes chaofa* sp. nov. (KS168)															
13	*Desmoxytes chaofa* sp. nov. (KS169)															
14	*Desmoxytes corythosaurus* (017)															
15	*Desmoxytes delfae* (M2)															
16	*Desmoxytes delfae* (M3)															
17	*Desmoxytes des* (DAK)	0.1063														
18	*Desmoxytes des* (KS154)	0.1061	0.0442													
19	*Desmoxytes des* (KS156)	0.1061	0.0442	0.0000												
20	*Desmoxytes euros* (160)	0.1769	0.1268	0.1294	0.1294											
21	*Desmoxytes euros* (161)	0.1769	0.1290	0.1309	0.1309	0.0043										
22	*Desmoxytes flabella* (212)	0.0980	0.1469	0.1320	0.1320	0.2001	0.2001									
23	*Desmoxytes flabella* (213)	0.0980	0.1469	0.1320	0.1320	0.2001	0.2001	0.0000								
24	*Desmoxytes golovatchi* (A4)	0.1205	0.1204	0.1109	0.1109	0.1325	0.1336	0.1043	0.1043							
25	*Desmoxytes golovatchi* (B15)	0.1212	0.1220	0.1140	0.1140	0.1366	0.1378	0.1083	0.1083	0.0046						
26	*Desmoxytes octoconigera* (A10)	0.1297	0.1047	0.1186	0.1186	0.1683	0.1703	0.1818	0.1818	0.1184	0.1250					
27	*Desmoxytes octoconigera* (A11)	0.1319	0.1048	0.1195	0.1195	0.1717	0.1739	0.1809	0.1809	0.1195	0.1270	0.0073				
28	*Desmoxytes pinnasquali* (055)	0.1157	0.1258	0.1253	0.1253	0.1606	0.1614	0.1554	0.1554	0.1023	0.1084	0.1193	0.1216			
29	*Desmoxytes pinnasquali* (059)	0.1157	0.1258	0.1253	0.1253	0.1606	0.1614	0.1554	0.1554	0.1023	0.1084	0.1193	0.1216	0.0000		
30	*Desmoxytes pinnasquali* (KS188)	0.1136	0.1309	0.1291	0.1291	0.1639	0.1646	0.1512	0.1512	0.1020	0.1078	0.1243	0.1267	0.0073	0.0073	
31	*Desmoxytes pinnasquali* (KS189)	0.1136	0.1309	0.1291	0.1291	0.1639	0.1646	0.1512	0.1512	0.1020	0.1078	0.1243	0.1267	0.0073	0.0073	0.0000
32	*Desmoxytes purpurosea* (002)	0.1501	0.1275	0.1173	0.1173	0.1040	0.1043	0.1708	0.1708	0.0986	0.1037	0.1536	0.1557	0.1245	0.1245	0.1191
33	*Desmoxytes purpurosea* (159)	0.1445	0.1085	0.1229	0.1229	0.0999	0.1002	0.1878	0.1878	0.1003	0.1027	0.1633	0.1668	0.1009	0.1009	0.1072
34	*Desmoxytes purpurosea* (A22)	0.1498	0.1268	0.1185	0.1185	0.1024	0.1024	0.1702	0.1702	0.0967	0.1014	0.1540	0.1563	0.1250	0.1250	0.1193
35	*Desmoxytes purpurosea* (119)	0.1150	0.1086	0.0899	0.0899	0.1559	0.1576	0.1198	0.1198	0.0664	0.0701	0.1143	0.1141	0.0868	0.0868	0.0851
36	*Desmoxytes purpurosea* (120)	0.1150	0.1086	0.0899	0.0899	0.1559	0.1576	0.1198	0.1198	0.0664	0.0701	0.1143	0.1141	0.0868	0.0868	0.0851
37	*Desmoxytes purpurosea* (126)	0.1184	0.1087	0.1017	0.1017	0.1492	0.1513	0.1209	0.1209	0.0692	0.0733	0.1196	0.1194	0.0794	0.0794	0.0777
38	*Desmoxytes sirindhornae* sp. nov. (KS159)	0.1118	0.1077	0.1120	0.1120	0.1777	0.1791	0.1178	0.1178	0.1273	0.1314	0.1347	0.1360	0.1152	0.1152	0.1133
39	*Desmoxytes sirindhornae* sp. nov. (KS160)	0.1118	0.1077	0.1120	0.1120	0.1777	0.1791	0.1178	0.1178	0.1273	0.1314	0.1347	0.1360	0.1152	0.1152	0.1133
40	*Desmoxytes sirindhornae* sp. nov. (KS161)	0.1118	0.1077	0.1120	0.1120	0.1777	0.1791	0.1178	0.1178	0.1273	0.1314	0.1347	0.1360	0.1152	0.1152	0.1133
41	*Desmoxytes sirindhornae* sp. nov. (KS162)	0.1118	0.1077	0.1120	0.1120	0.1777	0.1791	0.1178	0.1178	0.1273	0.1314	0.1347	0.1360	0.1152	0.1152	0.1133
42	*Desmoxytes takensis* (063)	0.1024	0.1037	0.0963	0.0963	0.1435	0.1441	0.1076	0.1076	0.0504	0.0527	0.1089	0.1095	0.0825	0.0825	0.0834
43	*Desmoxytes takensis* (064)	0.1024	0.1037	0.0963	0.0963	0.1435	0.1441	0.1076	0.1076	0.0504	0.0527	0.1089	0.1095	0.0825	0.0825	0.0834
44	*Desmoxytes takensis* (136)	0.0900	0.0987	0.0939	0.0939	0.1335	0.1343	0.1070	0.1070	0.0541	0.0559	0.1141	0.1154	0.0817	0.0817	0.0771
45	*Desmoxytes terae* (220)	0.1069	0.1019	0.0829	0.0829	0.1447	0.1447	0.1034	0.1034	0.1278	0.1325	0.1358	0.1365	0.1305	0.1305	0.1235
46	*Desmoxytes terae* (M9)	0.1069	0.1019	0.0829	0.0829	0.1447	0.1447	0.1034	0.1034	0.1278	0.1325	0.1358	0.1365	0.1305	0.1305	0.1235
47	*Desmoxytes waepyanensis* (143)	0.1052	0.0992	0.0843	0.0843	0.1208	0.1216	0.1035	0.1035	0.0627	0.0643	0.1364	0.1376	0.0837	0.0837	0.0860
48	*Desmoxytes waepyanensis* (144)	0.1051	0.0986	0.0838	0.0838	0.1210	0.1217	0.1035	0.1035	0.0635	0.0650	0.1362	0.1374	0.0828	0.0828	0.0852
49	*Gigaxytes gigas* (K1)	0.1520	0.1509	0.1725	0.1725	0.1723	0.1739	0.1875	0.1875	0.1948	0.2029	0.1381	0.1387	0.1548	0.1548	0.1566
50	*Hylomus rhinoceros* (E12)	0.1146	0.1470	0.1247	0.1247	0.2242	0.2242	0.1447	0.1447	0.1484	0.1534	0.1719	0.1721	0.2099	0.2099	0.2099
51	*Nagaxytes erecta* (C7)	0.1630	0.1388	0.1595	0.1595	0.2081	0.2090	0.1529	0.1529	0.1582	0.1677	0.1614	0.1634	0.1490	0.1490	0.1431
52	*Orthomorpha* cf. *pterygota* (K9)	0.1415	0.1479	0.1499	0.1499	0.1998	0.2007	0.1355	0.1355	0.1924	0.2015	0.1493	0.1501	0.1651	0.1651	0.1615
53	*Pogonosternum adrianae*	0.2361	0.1535	0.1720	0.1720	0.2347	0.2361	0.2291	0.2291	0.1752	0.1752	0.1974	0.1993	0.1511	0.1511	0.1511
54	*Pogonosternum laetificum*	0.2134	0.1694	0.1935	0.1935	0.2604	0.2617	0.2184	0.2184	0.1677	0.1677	0.2111	0.2129	0.1650	0.1650	0.1650
55	*Siamaxytes bifurca* (C14)	0.0860	0.1292	0.1242	0.1242	0.2036	0.2051	0.1243	0.1243	0.1566	0.1612	0.1521	0.1509	0.1566	0.1566	0.1594

APPENDIX

TABLE A1. Continued.

	Taxa	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
1	*Desmoxytes aurata* (095)															
2	*Desmoxytes aurata* (096)															
3	*Desmoxytes breviverpa* (048)															
4	*Desmoxytes breviverpa* (053)															
5	*Desmoxytes cervina* (B4)															
6	*Desmoxytes cervina* (B6)															
7	*Desmoxytes cervina* (B7)															
8	*Desmoxytes cervina* (K2)															
9	*Desmoxytes chaofa* sp. nov. (KS164)															
10	*Desmoxytes chaofa* sp. nov. (KS165)															
11	*Desmoxytes chaofa* sp. nov. (KS167)															
12	*Desmoxytes chaofa* sp. nov. (KS168)															
13	*Desmoxytes chaofa* sp. nov. (KS169)															
14	*Desmoxytes corythosaurus* (017)															
15	*Desmoxytes delfae* (M2)															
16	*Desmoxytes delfae* (M3)															
17	*Desmoxytes des* (DAK)															
18	*Desmoxytes des* (KS154)															
19	*Desmoxytes des* (KS156)															
20	*Desmoxytes euros* (160)															
21	*Desmoxytes euros* (161)															
22	*Desmoxytes flabella* (212)															
23	*Desmoxytes flabella* (213)															
24	*Desmoxytes golovatchi* (A4)															
25	*Desmoxytes golovatchi* (B15)															
26	*Desmoxytes octoconigera* (A10)															
27	*Desmoxytes octoconigera* (A11)															
28	*Desmoxytes pinnasquali* (055)															
29	*Desmoxytes pinnasquali* (059)															
30	*Desmoxytes pinnasquali* (KS188)															
31	*Desmoxytes pinnasquali* (KS189)															
32	*Desmoxytes purpurosea* (002)	0.1191														
33	*Desmoxytes purpurosea* (159)	0.1072	0.0464													
34	*Desmoxytes purpurosea* (A22)	0.1193	0.0118	0.0475												
35	*Desmoxytes purpurosea* (119)	0.0851	0.1053	0.1231	0.1068											
36	*Desmoxytes purpurosea* (120)	0.0851	0.1053	0.1231	0.1068	0.0000										
37	*Desmoxytes purpurosea* (126)	0.0777	0.1066	0.1210	0.1063	0.0232	0.0232									
38	*Desmoxytes sirindhornae* sp. nov. (KS159)	0.1133	0.1680	0.1615	0.1604	0.1294	0.1294	0.1346								
39	*Desmoxytes sirindhornae* sp. nov. (KS160)	0.1133	0.1680	0.1615	0.1604	0.1294	0.1294	0.1346	0.0000							
40	*Desmoxytes sirindhornae* sp. nov. (KS161)	0.1133	0.1680	0.1615	0.1604	0.1294	0.1294	0.1346	0.0000	0.0000						
41	*Desmoxytes sirindhornae* sp. nov. (KS162)	0.1133	0.1680	0.1615	0.1604	0.1294	0.1294	0.1346	0.0000	0.0000	0.0000					
42	*Desmoxytes takensis* (063)	0.0834	0.1227	0.1147	0.1225	0.0706	0.0706	0.0692	0.1163	0.1163	0.1163	0.1163				
43	*Desmoxytes takensis* (064)	0.0834	0.1227	0.1147	0.1225	0.0706	0.0706	0.0692	0.1163	0.1163	0.1163	0.1163	0.0000			
44	*Desmoxytes takensis* (136)	0.0771	0.1135	0.1203	0.1132	0.0664	0.0664	0.0652	0.1021	0.1021	0.1021	0.1021	0.0184	0.0184		
45	*Desmoxytes terae* (220)	0.1235	0.1502	0.1734	0.1519	0.1163	0.1163	0.1119	0.1005	0.1005	0.1005	0.1005	0.0883	0.0883	0.0812	
46	*Desmoxytes terae* (M9)	0.1235	0.1502	0.1734	0.1519	0.1163	0.1163	0.1119	0.1005	0.1005	0.1005	0.1005	0.0883	0.0883	0.0812	0.0000
47	*Desmoxytes waepyanensis* (143)	0.0860	0.1024	0.1134	0.1021	0.0637	0.0637	0.0609	0.1187	0.1187	0.1187	0.1187	0.0473	0.0473	0.0477	0.0857
48	*Desmoxytes waepyanensis* (144)	0.0852	0.1025	0.1136	0.1024	0.0636	0.0636	0.0609	0.1180	0.1180	0.1180	0.1180	0.0482	0.0482	0.0486	0.0853
49	*Gigaxytes gigas* (K1)	0.1566	0.2112	0.1973	0.2130	0.1506	0.1506	0.1629	0.1307	0.1307	0.1307	0.1307	0.1518	0.1518	0.1634	0.1536
50	*Hylomus rhinoceros* (E12)	0.2099	0.2478	0.2292	0.2441	0.1621	0.1621	0.1671	0.1762	0.1762	0.1762	0.1762	0.1448	0.1448	0.1354	0.1923
51	*Nagaxytes erecta* (C7)	0.1431	0.1805	0.2168	0.1809	0.1596	0.1596	0.1712	0.1430	0.1430	0.1430	0.1430	0.1518	0.1518	0.1403	0.1207
52	*Orthomorpha* cf. *pterygota* (K9)	0.1615	0.2072	0.2326	0.2025	0.1348	0.1348	0.1524	0.1302	0.1302	0.1302	0.1302	0.1512	0.1512	0.1324	0.1300
53	*Pogonosternum adrianae*	0.1511	0.2262	0.2149	0.2280	0.1762	0.1762	0.1666	0.2050	0.2050	0.2050	0.2050	0.1807	0.1807	0.1758	0.1707
54	*Pogonosternum laetificum*	0.1650	0.2537	0.2451	0.2543	0.1600	0.1600	0.1432	0.2480	0.2480	0.2480	0.2480	0.1715	0.1715	0.1604	0.1711
55	*Siamaxytes bifurca* (C14)	0.1594	0.1736	0.1756	0.1708	0.1392	0.1392	0.1436	0.1302	0.1302	0.1302	0.1302	0.1369	0.1369	0.1348	0.1234

APPENDIX

TABLE A1. Continued.

	Taxa	46	47	48	49	50	51	52	53	54
1	*Desmoxytes aurata* (095)									
2	*Desmoxytes aurata* (096)									
3	*Desmoxytes breviverpa* (048)									
4	*Desmoxytes breviverpa* (053)									
5	*Desmoxytes cervina* (B4)									
6	*Desmoxytes cervina* (B6)									
7	*Desmoxytes cervina* (B7)									
8	*Desmoxytes cervina* (K2)									
9	*Desmoxytes chaofa* sp. nov. (KS164)									
10	*Desmoxytes chaofa* sp. nov. (KS165)									
11	*Desmoxytes chaofa* sp. nov. (KS167)									
12	*Desmoxytes chaofa* sp. nov. (KS168)									
13	*Desmoxytes chaofa* sp. nov. (KS169)									
14	*Desmoxytes corythosaurus* (017)									
15	*Desmoxytes delfae* (M2)									
16	*Desmoxytes delfae* (M3)									
17	*Desmoxytes des* (DAK)									
18	*Desmoxytes des* (KS154)									
19	*Desmoxytes des* (KS156)									
20	*Desmoxytes euros* (160)									
21	*Desmoxytes euros* (161)									
22	*Desmoxytes flabella* (212)									
23	*Desmoxytes flabella* (213)									
24	*Desmoxytes golovatchi* (A4)									
25	*Desmoxytes golovatchi* (B15)									
26	*Desmoxytes octoconigera* (A10)									
27	*Desmoxytes octoconigera* (A11)									
28	*Desmoxytes pinnasquali* (055)									
29	*Desmoxytes pinnasquali* (059)									
30	*Desmoxytes pinnasquali* (KS188)									
31	*Desmoxytes pinnasquali* (KS189)									
32	*Desmoxytes purpurosea* (002)									
33	*Desmoxytes purpurosea* (159)									
34	*Desmoxytes purpurosea* (A22)									
35	*Desmoxytes purpurosea* (119)									
36	*Desmoxytes purpurosea* (120)									
37	*Desmoxytes purpurosea* (126)									
38	*Desmoxytes sirindhornae* sp. nov. (KS159)									
39	*Desmoxytes sirindhornae* sp. nov. (KS160)									
40	*Desmoxytes sirindhornae* sp. nov. (KS161)									
41	*Desmoxytes sirindhornae* sp. nov. (KS162)									
42	*Desmoxytes takensis* (063)									
43	*Desmoxytes takensis* (064)									
44	*Desmoxytes takensis* (136)									
45	*Desmoxytes terae* (220)									
46	*Desmoxytes terae* (M9)									
47	*Desmoxytes waepyanensis* (143)	0.0857								
48	*Desmoxytes waepyanensis* (144)	0.0853	0.0047							
49	*Gigaxytes gigas* (K1)	0.1536	0.1600	0.1591						
50	*Hylomus rhinoceros* (E12)	0.1923	0.1633	0.1633	0.1551					
51	*Nagaxytes erecta* (C7)	0.1207	0.1511	0.1508	0.2373	0.2651				
52	*Orthomorpha* cf. *pterygota* (K9)	0.1300	0.1559	0.1559	0.1346	0.1862	0.1614			
53	*Pogonosternum adrianae*	0.1707	0.1677	0.1674	0.2270	0.2208	0.1537	0.1770		
54	*Pogonosternum laetificum*	0.1711	0.1652	0.1644	0.2897	0.2063	0.1221	0.1821	0.0384	
55	*Siamaxytes bifurca* (C14)	0.1234	0.1276	0.1266	0.1505	0.1657	0.1424	0.1300	0.1558	0.1694

APPENDIX

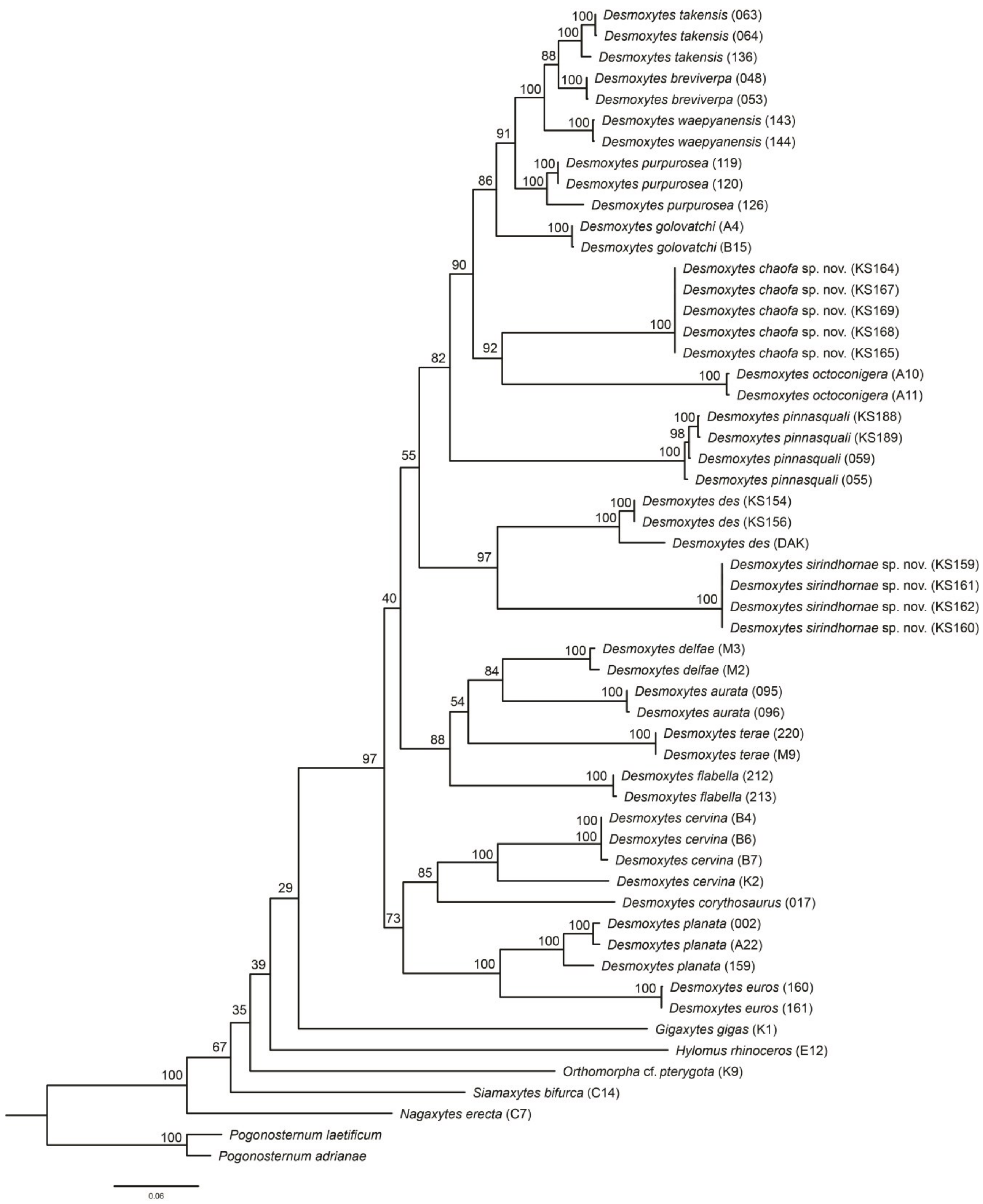

FIGURE A1. Phylogenetic tree based on maximum likelihood (ML) of the concatenated data set of three gene fragments.